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Regulation of transpiration water age by plant root-rock fissure interactions in epikarst

Xukun Zheng[a,b], Yuan Li [a,b,*], Qiuwen Zhou [a,b,*], Zidong Luo[c], Yi Chen[a] , Jun Zhang[c], Wenna Liu[c]

[a] School of Geography and Environmental Science, School of Karst Science, Guizhou Normal University, Guiyang 500025, China

[b] Guanling Karst Ecosystem Observation and Research Station, Guizhou Normal University, Guanling 561301, China

[c] Key Laboratory of Agro-ecological Processes in Subtropical Region, Institute of Subtropical Agriculture, Chinese Academy of Sciences, Changsha 410125, China

[*] Corresponding author at School of Geography and Environmental Science, School of Karst Science, Guizhou Normal University, Guiyang 500025, China.

Email addresses: liyuan7pro@163.com (Y. Li) and zqw@gznu.edu.cn (Q. Zhou)

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ABSTRACT

Under climate change, rock water becomes an important source of transpiration water for plants. However, in karst regions, rock fissure water and rooting depth are often not adequately considered in existing determination systems. This study conducted monthly field sampling over a year in a rock-dominated subtropical karst region, focusing on deep-rooted trees (*Ailanthus altissima* and *Juglans regia*) and shallow-rooted trees (*Zanthoxylum bungeanum* and *Eriobotrya japonica*). It integrated stable isotope tracing, the piecewise isotope balance method (quantifying the replenishment ratio of root-zone water), the piecewise linear mixing water age model (estimating the mean residence time of water utilized by plants), and geological drilling techniques. The results showed that rock fissure and root depth regulated the root zone water recharge rate of plants: deep-rooted trees (32%) were lower than shallow-rooted trees (44.3%) in the rainy season, while deep-rooted trees (10.4%) were higher than shallow-rooted trees (3.8%) in the dry season. Differences in water recharge to the root zone affected the age of plant transpiration: deep-rooted trees (46.4 d) were higher than shallow-rooted trees (35.1 d) during the rainy season, while the opposite was true during the dry season (deep-rooted trees: 139.6 d; shallow-rooted trees: 128.5 d). In addition, geological boreholes revealed that a large number of roots were distributed in rock fissures at a depth of 1.8-3.2 m below ground. The study showed that rock fissures are not only important channels for the formation of preferential flow in the rainy season, but also interact with the root system to regulate the water recharge in the root zone of plants and thus influence the change of transpiration water age, which provides a new perspective to understand the complex hydrological processes in karst areas.

Keywords: Karst; Epikarst; Rock fissures; Root zone recharge; Transpiration water age

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1. Introduction

Climate change is driving shifts in terrestrial ecosystems and accelerating changes in the terrestrial water cycle globally by altering precipitation patterns and increasing temperatures (Feldman et al., 2024; Yuan et al., 2023). Plants, as an important link between the soil and the atmosphere, account for more than 60% of terrestrial evapotranspiration (Schlesinger and Jasechko, 2014). Such a high transpiration flux is largely dependent on water recharge from root zone soil water (Luo et al., 2023). However, the root zone water transport and retention processes are crucial for plant water use strategies in response to climate change. Therefore, an in-depth understanding of the dynamics of water recharge status and transpiration water age (i.e., water residence time) in the root zone of plants is important for revealing how vegetation responds to hydroclimatic disturbances.

Hydrogen and oxygen isotopes (δ^2H and $\delta^{18}O$) have been widely used as natural tracers to quantify the process of water uptake by plants.Using stable isotope studies, Brooks et al. (2010) found that even when the root zone is well recharged with water, there is still a difference in the source of plant transpiration water versus runoff or groundwater (Evaristo et al. 2015; Good et al. 2015; Luo et al. 2019). However, inferences relying solely on differences in isotopic signatures between xylem water and groundwater are prone to bias (Sprenger and Allen, 2020). For this reason, Luo et al. (2022) emphasised that research should focus on the root zone water transport process, which not only helps to capture the dynamic characteristics of root zone water recharge, but also provides a new perspective for resolving the mechanism of transpiration water age change in different seasons.

Early ecohydrological studies focused on isotopic differences between plant xylem water and surrounding groundwater or stream water (Brooks et al., 2010; Evaristo et al., 2015; Zhao et al., 2018). When xylem water isotope signatures do not match known soil water, this is often attributed to "isotope fractionation" or "mixing effects" (Barbeta et al., 2019; Pfister et al., 2017). It is only in recent years that researchers have come to recognise the importance of rock weathering layers as a vast but long-neglected reservoir (Dawson et al., 2020). The isotope mismatch likely stems from the lack of rock water isotope data (Bowling et al., 2017; Geris et al., 2017). Several studies have shown

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that rock water storage sometimes contributes even more than saturated soil water to plant transpiration (Barbeta and Peñuelas, 2017), making it a key source of water for trees in response to drought stress (Rempe and Dietrich, 2018; Miguez-Machoa and Fan,2021; Klos et al. 2018; Hahm et al., 2022).

However, there is significant geomorphological differentiation in the strength of rock water contributions to plant root zone water recharge (Leite et al., 2025). Its availability is controlled by a combination of climatic conditions, degree of bedrock weathering, and density and depth of fracture development (Burns et al., 2023; Dawson et al., 2020; Liu et al., 2025b). Therefore, to gain insight into the central role of rock water in root zone water recharge, it must be examined in a specific geological context. In this context, the karst critical zone, with its shallow soils and typical "rock-soil" dichotomy (Behzad et al., 2023), significantly enhances the hydrological function of rock water, making it an ideal case for revealing the ecohydrological role of bedrock weathering layers. The Epikarst is the core hydrological unit in this area (Fig. 1), and the rock fissure water contained therein constitutes an "invisible reservoir" that plays a key role in regulating plant growth (Jiang et al., 2020; Deng et al., 2021; Nardini et al., 2021) and profoundly affects root zone hydrological processes. Although the importance of rock water for plants is widely recognised, the mechanism of interaction between direct access to rock fissure water and quantification of its recharge to the plant root zone remains unclear.

In karst habitats, plants often develop typical 'dimorphic' root systems, characterised by a uniform distribution and high density of fine roots in soil and bedrock, which are capable of absorbing water from different media (Cai et al., 2025). Coarse root systems of different depths (e.g., deep-rooted vs. shallow-rooted trees) determine the depth of water uptake by a plant (Savi et al., 2017; Zhou et al., 2020), which in turn affects the water age of the water to which it is exposed (Sprenger et al., 2019). Research suggests that the interaction between root distribution depth and water infiltration dynamics may lead plants to utilise past season precipitation more than recent precipitation (Allen et al., 2019), a phenomenon that has been demonstrated in both arid regions (Kerhoulas et al.,

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2013) and Mediterranean climatic zones (Brooks et al., 2010; Rempe and Dietrich, 2018) have been reported. However, most of the current studies on water age have focused on soil water, and attention to rock water as a source of water for root uptake is still insufficient. Especially in karst areas where the development of epikarst (bedrock weathering zones) is typical, studies on how rock fissure water regulates the transpiration water age of plants with different rooting depths are still relatively lacking.

This study addresses the following question: How do the interactions between vegetation root systems and rock fissure water at different depths regulate the dynamics of root zone water recharge in the karst epikarst, and thus affect the seasonal characteristics of plant transpiration water age? Therefore, we propose two scientific hypotheses: (i) In the epikarst, the active regulation of water uptake by plant roots and their extension into rock fractures to explore water sources is a key process governing the seasonal dynamics of root-zone water replenishment; (ii) Seasonal variations in plant transpiration water age are primarily driven by the dynamics of root-zone water replenishment. Specifically, increased replenishment leads to greater plant use of "new water," resulting in younger water ages, whereas decreased replenishment forces plants to rely more on "old water," leading to older water ages. Based on these hypotheses, this study aims to systematically validate the regulatory effects of the interaction between rock fractures and root depth on root-zone hydrological processes and their impact on plant transpiration water age, thereby elucidating the underlying driving mechanisms and providing a theoretical foundation for a deeper understanding of root-zone hydrological processes in karst regions.

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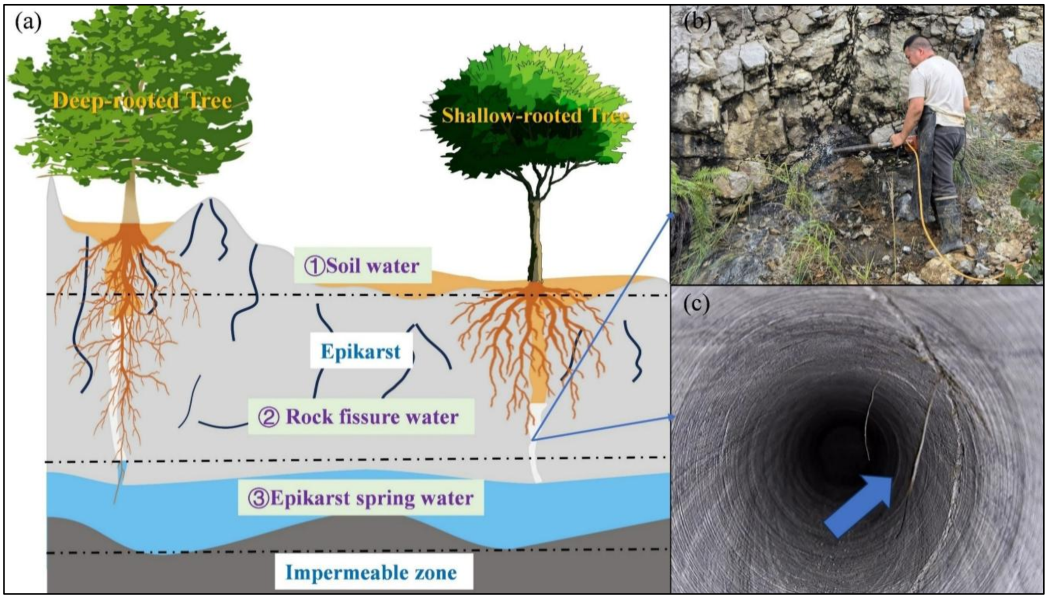

Fig. 1. Schematic diagram of plant water source classification in karst ecosystem. Where ① in (a) represents soil water, ② is rock fissure water, and ③ is epikarst spring water. It should be noted that the rocks in the area are hard and deep, and numerous studies in the area have used artesian springs instead of groundwater. (b) shows the process of perforating rock fissures in the epikarst, where we drilled diagonally down the broken rock fissure zone for the purpose of collecting fissure water. (c) shows the fine roots of plants found growing in the rock fissure holes during our sampling.

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2. Materials and methods

2.1. Study area

This study was conducted in the Dingtan catchment area of the Huajiang Canyon in the Zhenfeng-Guanling karst plateau canyon, Guizhou Province (Fig. 2b), which is affiliated with the Guanling Karst Ecosystem Field Scientific Observation and Research Station. The study area ranges in altitude from 450 to 1300 meters, with Triassic dolomitic limestone as the main bedrock. Intense karstification has formed a dense vertical fracture network. The surface is covered with calcic soil and mountain yellow soil, with an average thickness of only 26 cm (Li et al., 2020, 2022). The region has a subtropical humid monsoon climate, with an annual average temperature of 18.4 °C and an annual precipitation of approximately 1100 mm, with over 80% of the annual precipitation concentrated from May to October. The land use types include cultivated land, forest land, and abandoned land. In the late 20th century, deforestation for farming led to severe soil erosion, with rock exposure rates as high as 70% (Yan and Cai, 2015). With the implementation of ecological protection policies, the current vegetation is mainly artificial mixed forests, including walnut mixed forests, bamboo mixed economic forests, and fir mixed economic forests, and the community structure shows a recovery trend (Cai et al., 2023).

The study area features a complex karst canyon landscape, and its hydrogeological structure is typical and representative of the karst regions in southwest China. The development of the epikarst is closely related to the evolution of the canyon: driven by neotectonic movements, the regional crust has undergone intense uplift and the base level has continuously dropped, causing the river to deeply incise and form a more than 800-meter-deep sheer-walled canyon system. This has led to a lowering of the groundwater level and an increase in the thickness of the epikarst. The Dingtan small watershed is located within the epikarst on the southwest side of the canyon, in areas with well-developed joints or fractures with good permeability. Under the force of gravity, water seeps vertically to form a vertical fracture network (Fig. 2f). This unique rapid water-conducting characteristic of the karst medium makes this area a natural laboratory for studying the ecohydrological processes in the

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epikarst.

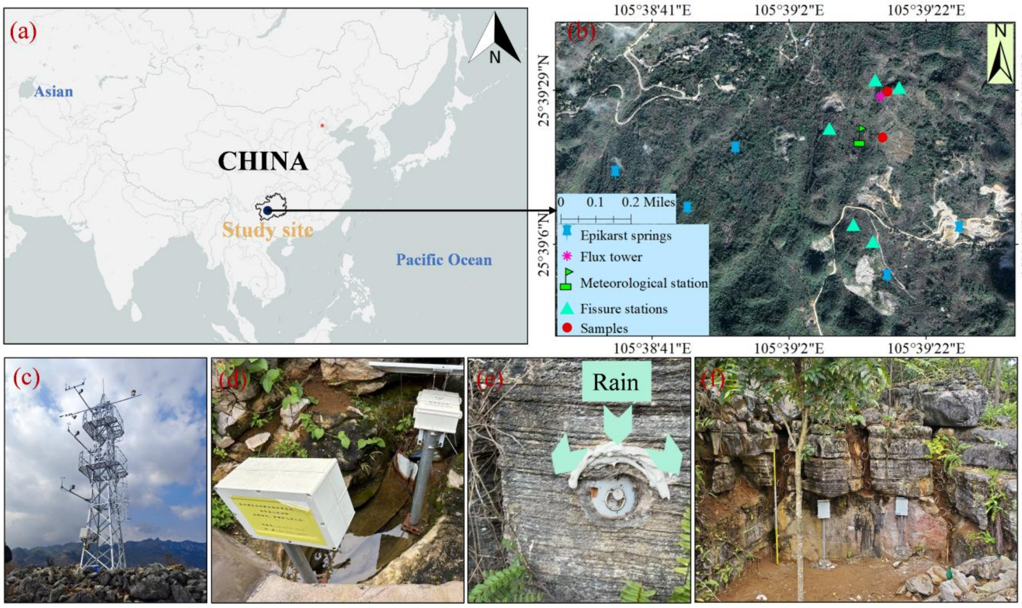

Fig. 2. Overview of the study area. (b) shows the locations of rock fissure points, meteorological stations, eddy covariance system flux towers, epikarst springs, and sample plots. (c) is the eddy covariance system flux tower used to monitor evapotranspiration in the study area. (d) is an exposed epikarst spring. (e) The white object above the fissure hole is glass glue, which, after air-drying and solidifying, functions as a water diversion channel to reduce the impact of rainwater on the rock wall on the isotopes inside the hole. (f) is a sample point in epikarst. Aerial satellite image source: https://www.91weitu.com/.

2.2. Sample design

2.2.1 Plot Information

Our previous observational work indicates that shrubs have relatively shallow root systems and a single water absorption layer, while tree species have deeper and more diverse root systems (Cai et al., 2023, 2025). The differences in root structure between the two types of plants result in distinct water competition strategies in the epikarst. Therefore, this study selected four dominant woody plants in the study area as research subjects - *Ailanthus altissima*, *Juglans regia*, *Eriobotrya japonica*, and *Zanthoxylum bungeanum*. The diameter at breast height (DBH) and tree height parameters of these plants are shown in Table 1. The plots where the plants are located are less than 100 meters

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apart. The altitude is similar, and the water and heat conditions and community structure are basically the same (Cai et al., 2025b).

Table 1 Brief Information of Four Tree Species in the Study Area

Species	Family	Life form	Leaf habit	DBH(cm)	Height(m)
Ailanthus altissima	Simaroubaceae	deep root	deciduous	47.8±2.75	11.8±0.8
Juglans regia	Juglandaceae	deep root	deciduous	25.8±2.95	6.9±0.8
Zanthoxylum bungeanum	Rutaceae	shallow root	evergreen	3.8±0.88	2.5±0.5
Eriobotrya japonica	Rosaceae	shallow root	evergreen	8.4±0.35	3.4±0.4

2.2.2 Sample Collection

From July 2024 to July 2025, we conducted monthly sampling to systematically collect samples of plant xylem, soil, water from rock fissures, and epikarst spring water (groundwater) for hydrogen and oxygen isotope analysis. The method for collecting xylem samples was as follows: from three standard trees of each plant species, healthy branches in different directions of the tree crown were selected, and stem segments with a diameter of approximately 10 mm and a length of 50-80 mm were cut. The phloem was quickly stripped to prevent isotope contamination. Each tree was divided into three samples and placed in 12 mL glass bottles, which were then sealed and stored at low temperatures. Soil samples were collected in vertical layers of 0-10 cm, 10-20 cm, 20-30 cm, and 30-40 cm within a radius of 0.5 m around the roots of each plant. A manual auger was used to drill into each soil layer successively, and three independent samples were taken from each layer. These samples were thoroughly mixed and placed in glass bottles for isotope determination. Undisturbed soil cores were also collected and placed in aluminum boxes to measure soil water content (SWC, %) using the oven-drying method (105 °C for 24 hours) until a constant weight was achieved.

In the study area, 36 vertical fissures in the epikarst were selected. A geological drill was used to drill vertically along the fissure trend (Fig. 1 and 2e), with a hole diameter of 50 mm and a depth of 1 m. After drilling, the hole mouth was sealed with a silica gel plug and coated with epoxy resin on the outside to enhance the sealing effect, effectively preventing evaporation from the atmosphere

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and lateral infiltration of precipitation, ensuring the authenticity of the isotope signal of the rock fissure water. Loose cotton was loosely filled to the bottom of the drill hole, and its capillary adsorption effect was utilized to continuously collect fissure water or water vapor. During each sampling, the cotton along with the water was sealed in a glass bottle and stored at low temperatures. In response to the risk of fractionation that may be caused by the isotopes of skimmed cotton itself, Zhao and Wang (2025) pointed out that skimmed cotton fibres cause significant shifts in δ^2H and $\delta^{18}O$ values when the sample volume of low-temperature vacuum extraction (CVD) is <0.5 mL; whereas, the sample extraction volumes of the samples of the present study were all >1 mL, and the adsorptive interference of the skimmed cotton under this condition can be negligible (Diao et al., 2022). In addition, the potential contamination risk was further reduced by removing the residual organic matter from the degreasing cotton by autoclaving (200 °C, 2 h) before using the degreasing cotton.

Five perennially exposed natural epikarst spring points within the spring basin where the sample plots were located were selected as alternative sampling points for groundwater (Fig. 2d). This method is in line with the conventional practice for studying the water sources of plants in karst areas (Nie et al., 2012; Deng et al., 2015; Cai et al., 2023).

2.2.3 Meteorological Parameter Observation

A meteorological station (ATMOS, METER Group Inc., USA) was set up within 100 m of the sample plot, automatically recording air temperature (°C), precipitation (mm), and relative humidity (%) every 30 minutes. An eddy covariance system (CPEC310, Campbell Scientific, Inc., USA) was installed in the study area to monitor evapotranspiration (Fig. 2c). A high-density electrical method (ABEM, Terrameter LS2, USA) was used to invert the water content beneath the vegetation in the sample plot through the least squares method. Typical species were selected in the study area (For further details, see Table A1), including deep-rooted trees: *Ailanthus altissima*, *Juglans regia*, and *Koelreuteria paniculata*; and shallow-rooted trees: *Zanthoxylum bungeanum*, *Eriobotrya japonica*, and *Broussonetia papyrifera*. Precipitation samples were collected using an automatic rainfall collector (Laoying-5020, Hainuo Optoelectronic Environmental Protection Group Co., Ltd., Qingdao,

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China), which was equipped with a built-in refrigeration module (constant temperature at 4 ℃) to inhibit evaporation fractionation and could capture rainfall events greater than 0.1 mm. During the study period, the average daily temperature in winter was above 0 ℃ (Fig. 4a), and no snowfall interference occurred, ensuring that the precipitation isotope data only reflected the characteristics of liquid rainfall. All samples were immediately sealed with Parafilm after collection, refrigerated at 4 ℃, and transported to the laboratory until isotope analysis was completed.

2.3. Isotope Analysis

Water extraction of plant xylem, soil and rock fissure water samples was carried out using a low-temperature vacuum distillation system (LI-2100, LICA United Technology Ltd., Beijing, China) for 3 h, with a water extraction rate of > 98%. The extracted water samples were filtered through a 0.22 μm filter membrane to remove suspended particles and then transferred to 2 mL clean sample bottles using a 1000 μL high-precision pipette. At the National Engineering Research Center for Karst Desertification Control, the δ^2H and $\delta^{18}O$ values were determined using a liquid water isotope analyzer (T-LWIA-45-EP, Los Gatos Research Inc., California, USA). To address the potential spectral interference in plant xylem, the original data were corrected (for details, see Cai et al., 2025b). All samples were measured six times, with the first two results excluded to minimize memory and drift effects (Oerter and Bowen, 2017). The results were calibrated against Vienna Standard Mean Ocean Water (V-SMOW) using the following formula:

$$\delta = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000 \quad (1)$$

In the formula, δ(‰) represents the ratios of $^2H/H$ and $^{18}O/^{16}O$, and R is the ratio of the sample to standard seawater. The analytical precision of the instrument is δ^2H ± 0.3‰ and $\delta^{18}O$ ± 1‰ respectively.

2.4 Methods for estimating root zone water recharge and water age modelling

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Piecewise isotope balance (PIB) was used to capture plant root zone water dynamics. By quantifying the proportion (β, %) of plant-available water recharge in the root zone between successive precipitation events, we reveal the mechanism of recharge or preferential flow bypassing process of precipitation infiltration on root zone water (Luo et al., 2019). We assumed that precipitation is the main recharge water source for plants, and combined with related literature evidence found that hydrogen isotopes (δ^2H) may be fractionated during xylem transport (Zhao et al., 2016; Barbeta et al., 2019), so oxygen isotopes ($\delta^{18}O$) were chosen as a reliable indicator for β value calculation. The formula is as follows:

$$\beta = \left(\delta_{x,i} - \delta_{x,i-1}\right) / \left(\delta_{\sum \rho} - \delta_{x,i-1}\right) \times 100\% \tag{2}$$

Where $\delta_{x,i}$ and $\delta_{x,i-1}$ represent the $\delta^{18}O$ value of plant stem water during two consecutive sampling events, and $\delta\sum_{\rho}$ represents the precipitation $\delta^{18}O$ value weighted by the amount of precipitation during the two consecutive sampling periods (a single rainfall event may be divided into several smaller events, and it is necessary to combine the amount of rainfall with the weighted average of each rainfall event to compute the $\delta^{18}O/\delta^2H$ value of a single rainfall event). β is defined as 0 when $\delta_{x,i} < \delta_{x,i-1}$ and $\delta\sum_p > \delta_{x,i-1}$ and as 0 when $\delta_{x,i} > \delta_{x,i-1}$ and $\delta\sum_p < \delta_{x,i-1}$. It is worth noting that β is defined as 0 when the soil water content is fairly high and does not change much between sampling events and the difference between $\delta_{x,i}$ and $\delta_{x,i-1}$ is very small in the short term (less than the $\delta^{18}O$ error ±0.3‰), β is defined as 0.

In addition, we calculate the water age of plant transpiration by combining the root zone recharge rate (β), thereby quantifying the average residence time of the recharge water in the root zone water storage. The higher the proportion of precipitation replenishing the root zone water, the newer the root zone water, that is, the shorter the average residence time of the root zone water. This indicator can effectively reflect the impact of ecohydrological separation on plants. As shown in Fig. (3), the calculation formula is based on the following assumptions (see Luo et al., 2023): First, the calculated β and the water age of transpiration water are a linear mixture of the water ages of "old water" and newly replenished water; second, $A_t(t_0)$ = 0 d, and the average residence time at the first sampling

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date t_1 is the time lag between t_0 and t_1($A_t(t_1) = t_1 - t_0$), to estimate the water age (A_t) in plant transpiration.

$$A_t(t_i) = A_p(t_i) \times \beta + [A_t(t_{i-1}) + \Delta t] \times (1 - \beta) \quad (3)$$

$$A_p(t_i) = t_i - \sum_{1}^{k}(t_k \times P_k) \Big/ \sum_{1}^{k} P_k \quad (4)$$

Here, $A_t(t_i)$ and $A_t(t_{i-1})$ represent the water age of plant transpiration at time steps t_i and t_{i-1} respectively, $A_p(t_i)$ indicates the water age of newly replenished water to transpiration at time step t_i, k is the number of precipitation events, t_k and P_k are the occurrence time and precipitation amount of the k_{th} precipitation event respectively, and $\Delta t = t_i - t_{i-1}$.

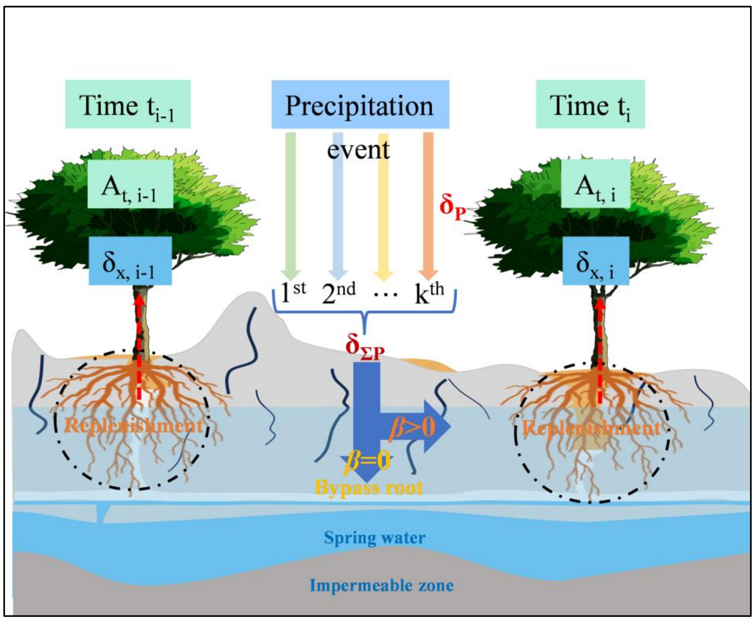

Fig. 3. Piecewise linear mixing water age model. Based on the study of the isotopic composition of plant xylem water and precipitation, a segmented linear mixed water age model was developed, and the related equations are Eq. 3 and Eq. 4. Note: When $\beta > 0$, it indicates that precipitation recharges the root zone; when $\beta < 0$, precipitation bypasses the root zone. Where $A_t(t_i)$ and $A_t(t_{i-1})$ are the water age of plant transpiration at time steps t_i and t_{i-1}, respectively, $A_p(t_i)$ denotes the water age of new replenishment to transpiration at time step t_i, k is the number of precipitation events, t_k and P_k are the time of occurrence of the k_{th} precipitation event and the amount of precipitation, respectively, $\Delta t = t_i - t_{i-1}$.

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3. Results

3.1. The meteorological conditions

The precipitation in the study area shows a significant seasonal imbalance. The total annual rainfall is 1289.3 mm, with 1215.7 mm falling during the rainy season (July to October 2024 and May to July 2025), while only 73.6 mm occurs during the dry season (November to April of the following year) (Fig. 4). There are obvious seasonal differences in the isotopic values of precipitation: δ^2H and $\delta^{18}O$ values are relatively depleted during the rainy season (−59.7‰ and −8.2‰ respectively), while they are more enriched during the dry season (δ^2H: 10.5‰, $\delta^{18}O$: −0.8‰). Relative humidity decreases with increasing temperature, averaging 75.9% during the rainy season and 71.5% during the dry season (Fig. 2b). The regional evapotranspiration is significantly higher during the rainy season (average 130.7 mm per month) than during the dry season (average 22.1 mm per month). Soil moisture varies with depth and season (Fig. 2c), with the average soil moisture content under plants being higher during the rainy season (29%) than during the dry season (24.8%).

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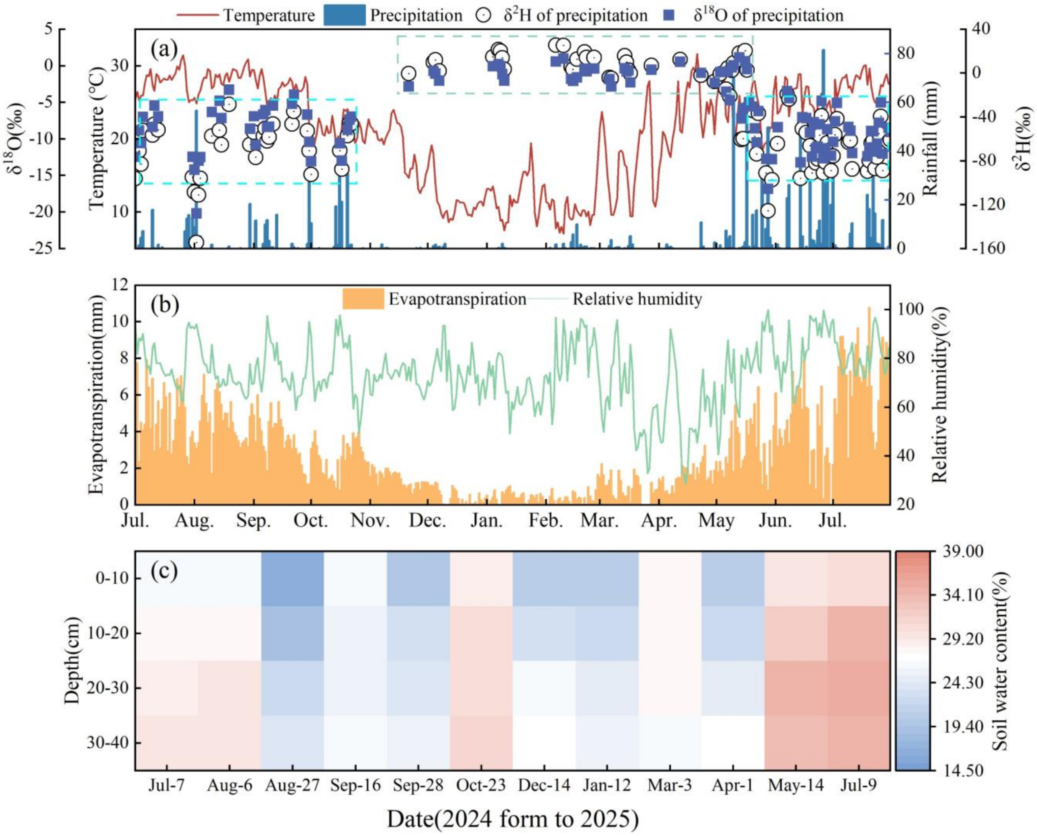

Fig. 4. Environmental conditions during the study period, including (a) isotopic values of rainwater temperature, and precipitation, (b) regional evapotranspiration and relative humidity, and (c) soil moisture content in the sampling months. The green and blue dashed boxes represent the δ^2H and $\delta^{18}O$ values of precipitation during the rainy and dry seasons, respectively. Note: Due to power outages caused by weather conditions, some data on regional evapotranspiration are missing (2024/12/11, 12/12, 12/18, 12/20, 12/22, 12/27; 2025/1/8, 1/22, 2/2, 2/20, 2/22, 3/23-3/27).

3.2. Seasonal variation of isotopes in different water sources

The hydrogen and oxygen isotope values of each pool and their seasonal variation characteristics during the research period. As shown in Fig. 5: All pools exhibited the pattern of isotope depletion in the rainy season and enrichment in the dry season. The weighted average isotope values of rainwater were δ^2H: -63.6‰ and $\delta^{18}O$: -8.5‰ in the rainy season, while they were significantly enriched in the dry season (δ^2H: 9.1‰, $\delta^{18}O$: -1.3‰). The δ^2H of deep-rooted and shallow-rooted tree xylem water

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ranged from -65.9‰ to -57.6‰ and δ¹⁸O from -8.5‰ to -6.8‰ in the rainy season; in the dry season, they were -59.7‰ to -52.9‰ and -7.3‰ to -5.7‰ respectively. Soil water had the largest isotope fluctuation amplitude (SD = 17.9), and the δ²H of rock fissure water ranged from -71.0‰ to -45.2‰, with δ¹⁸O from -8.1‰ to -4.3‰. Spring water had the most stable isotope values (δ²H: -56.8‰, δ¹⁸O: -8.0‰; SD = 5.6), reflecting its better mixing.

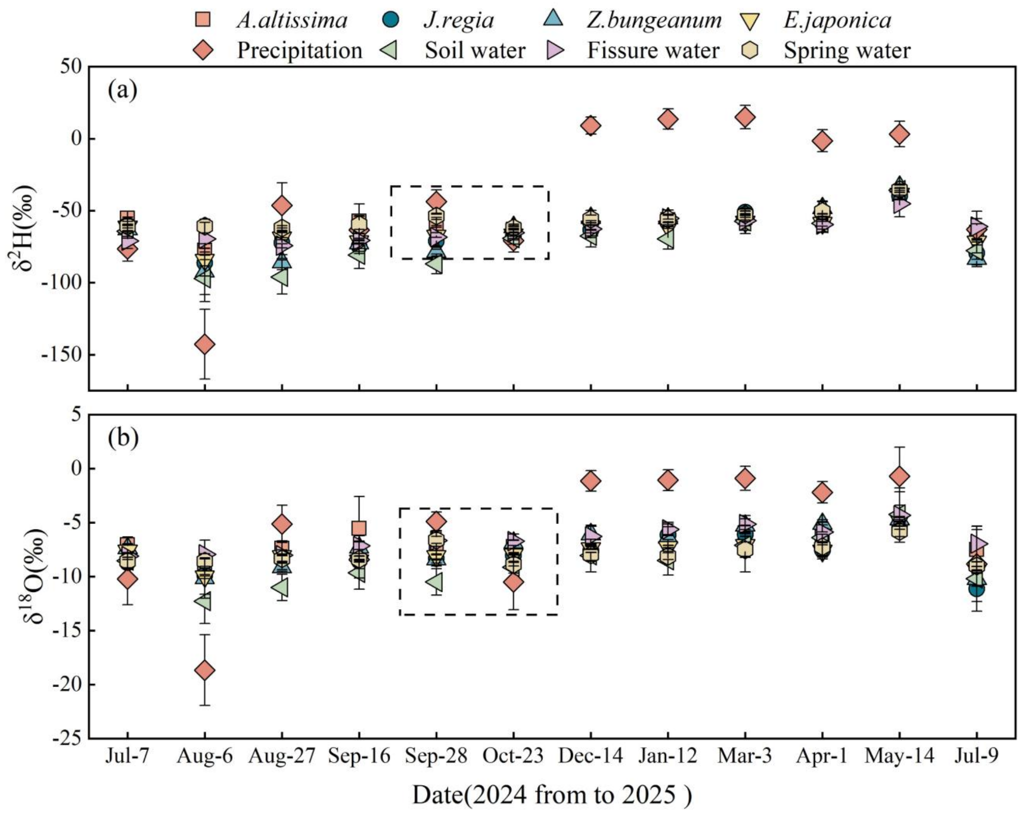

Fig. 5. Seasonal variation characteristics of hydrogen and oxygen isotopes in different water sources. (a) Distribution characteristics of hydrogen isotope values of xylem, soil, rock fissure water, spring water and weighted rainwater during the sampling period for *Ailanthus altissima*、*Juglans regia*、*Eriobotrya japonica* and *Zanthoxylum bungeanum*. (b) Distribution characteristics of oxygen isotope values. Note: The dotted box represents the distribution of hydrogen and oxygen isotope values of rainwater and plants when the root water supply rate was 0% on September 28th and October 23rd.

3.3. Dynamics of water recharge in the plant root zone

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Based on the segmented isotope balance method, the dynamic changes in water supply to the plant root zone in the karst surface karst zone were revealed (Fig. 6). During the observation period, the precipitation showed a fluctuating downward trend, and the water supply rate (β) in the plant root zone gradually decreased overall. The β values of the four plants during the rainy season (*Z. bungeanum*: 44.7%, *J. regia*: 36.5%, *A. altissima*: 27.5%, *E. japonica*: 44%) were significantly higher than those during the dry season (*Z. bungeanum*: 4.2%, *J. regia*: 9.4%, *A. altissima*: 11.3%, *E. japonica*: 3.3%), reflecting the impact of reduced precipitation in the later period of the rainy season on water supply to the root zone. The root zone water supply was 0% mainly occurring in two periods: one was the strong precipitation stage at the end of the rainy season, when the precipitation reached its peak in October, the supply rates of all four species dropped to 0%; the other was the high evaporation period at the end of the dry season, when the above situation occurred again for walnut, willow and loquat. No situation was found where the soil moisture content was extremely high and the changes in the wood parenchyma isotope values during the two sampling periods were not significant. Overall, the hydrological connectivity of deep-rooted trees in the rainy season was lower than that of shallow-rooted trees, while the opposite was true in the dry season, which may be related to the depth of the plant roots and the water utilization strategies.

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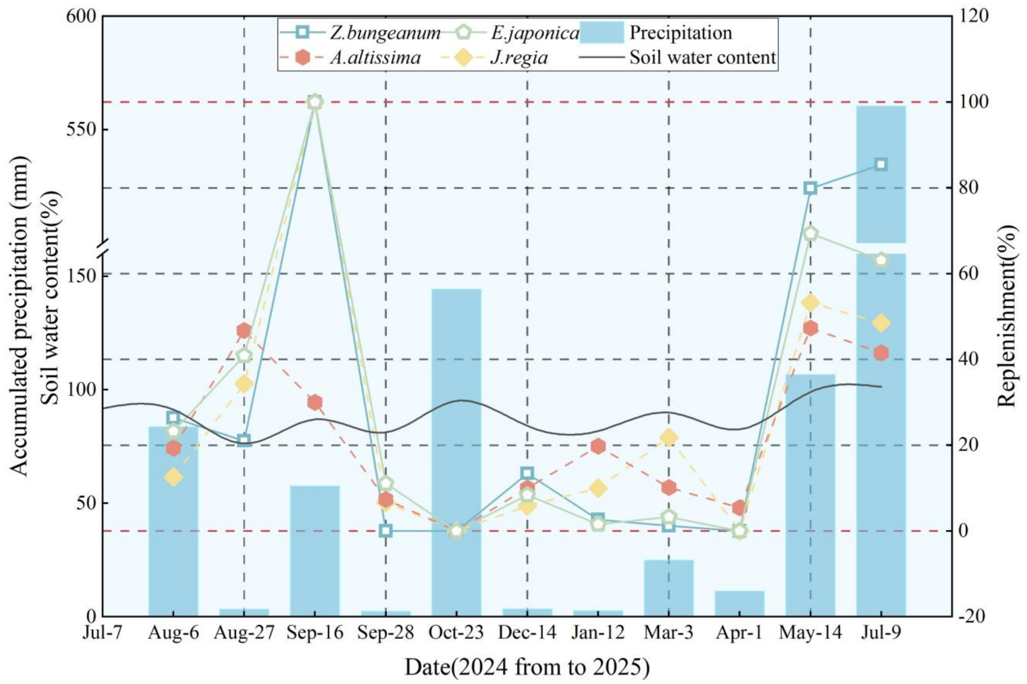

Fig. 6. Water recharge in the root zone and cumulative precipitation for four plant species between two consecutive samplings. The deep-rooted plants were *A. altissima* and *J. regia*; the shallow-rooted plants were *Z. bungeanum* and *E. japonica*. Note: The soil water content line in the figure shows the average soil water content of the four plants at each sampling; sampling was not conducted in February of the following year due to weather conditions.

3.4. Seasonal changes in the transpiration water age of plants

The fluctuations in plant transpiration water age are mainly driven by seasonal variations in precipitation (Fig. 7). During the rainy season, the range of plant transpiration water age varies from 10.4 days to 67.8 days; during the dry season, due to the increase in transpiration water age, it generally ranges from 87.2 days to 192.2 days. This difference in transpiration water age is mainly caused by the seasonal variation in water supply in the root zone. Higher β values are generally found during longer rainy seasons, when there is sufficient time for rainwater to infiltrate and replenish the root zone, resulting in a "newer" transpiration water age for plants; while if the precipitation intensity is too high or high evapotranspiration occurs, preventing effective replenishment of the root zone by

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rainwater ($\beta = 0\%$), the transpiration water age will be prolonged, but this situation is only temporary. There are no significant differences in the transpiration water age of the four plants within the same season ($p > 0.05$), but there are significant differences between different seasons ($p < 0.05$) (Fig. 8). The average transpiration water age of deep-rooted trees during the rainy season is 46.4 days, and that of shallow-rooted trees is 35.1 days; during the dry season, they are 139.4 days and 128.5 days respectively.

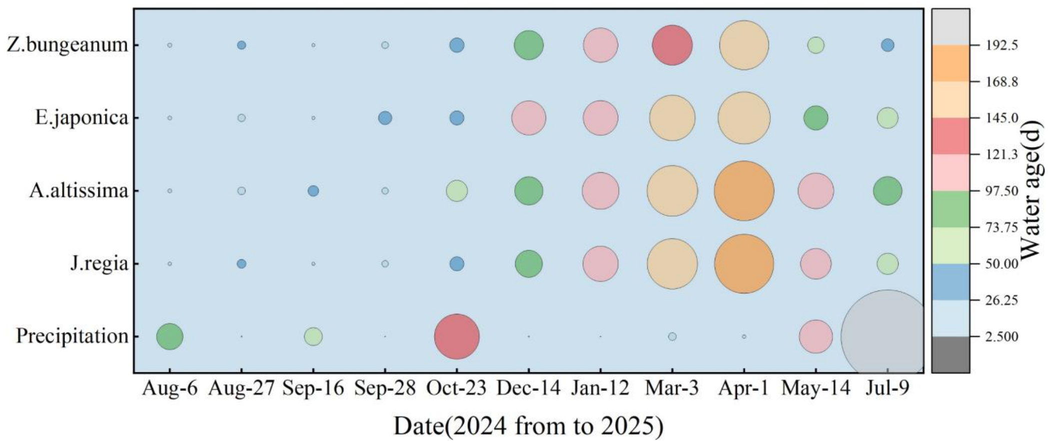

Fig. 7. Plant transpiration water age change characteristics. Where precipitation is the accumulated precipitation between two consecutive sampling periods. Note: The grey shading in the lower right corner of the figure shows the total accumulated precipitation from 14 May 2025 to 9 July 2025, which totalled 560.5 mm; no sampling was conducted in February of the following year due to weather conditions.

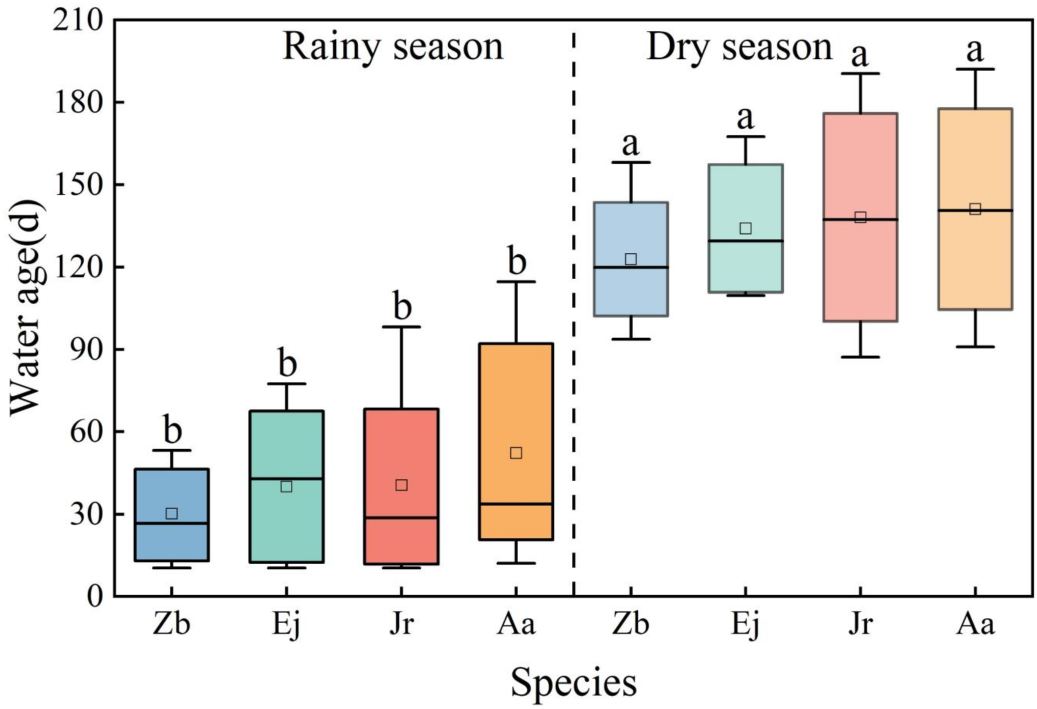

Fig. 8. Significance analysis of transpiration water age of plants in different seasons. Where Zb is *Z. bungeanum*, Ej is *E. japonica*, Jr is *J. regia*, and Aa is *A. altissima*. Note: Different letters indicate $p < 0.05$, while the same letter is not significant.

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4. Discussion

4.1. Influence of rock fissures and root depth on water recharge patterns in the root zone

This study reveals that the combined effect of plant root depth and rock fissures is a key factor in regulating the water recharge pattern in the root zone of karst epikarst (Fig. 6, A1, A3, A4). Deep-rooted plants are able to penetrate rock layers to access fissure water and groundwater directly (Schwinning, 2020; Querejeta et al., 2021; Liu et al., 2025a), whereas shallow-rooted plants are more dependent on soil water, and the two form distinct water use pathways. Rock fractures not only provide direct water pathways for plants (Ringrose-Voase and Nadelko, 2013; Wopereis et al., 1994), but also form a massive "hidden reservoir" (Jiménez-Rodríguez et al., 2022). This reservoir stores precipitation during the rainy season and sustains water supply throughout the dry season, thereby functioning as a pivotal regulator of root-zone water replenishment dynamics. It is worth noting that rock fissures not only act as natural conduits for root extension, but also provide shelter from environmental extremes (Pawlik et al., 2016; Zhang et al., 2016; Preisler et al., 2019).

Research indicates that epikarst vegetation experiences seasonal hydrological disconnection from recent precipitation, preventing timely plant uptake of rainfall. Instead, water rapidly bypasses the root zone via preferential flow or is lost to evaporation before reaching the roots, forcing plants to consistently rely on older water sources with longer residence times (Figure 6). In karst regions, the widespread rock-soil composite structure (Li et al., 2025; Li et al., 2022) and dense fracture-conduit networks cause shallow soils to saturate rapidly during short-duration, high-intensity rainfall events. Consequently, substantial amounts of precipitation rapidly infiltrate and are lost along dominant pathways (Zhang et al., 2025), failing to effectively replenish the root zone (i.e., $\beta = 0\%$). This process is reflected in the stable isotopic composition of plant xylem water across consecutive sampling events, even as the isotopic signature of concurrent precipitation shows significant variation (Figure 5). This phenomenon aligns with the widespread preferential flow processes previously observed in this region (Li et al., 2020).

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The hydrological disconnection during the dry season is controlled by a different mechanism. Although water consumption is generally low during most of the dry season, and limited precipitation can still replenish the root zone, rising temperatures towards the end of the dry season cause a sharp increase in evapotranspirative demand. Consequently, the limited precipitation is largely consumed by surface evaporation, making effective infiltration into the root zone difficult (Luo et al., 2022). Plants are thus forced to continuously rely on "older" water with longer residence times (Dubbert et al., 2019; Pei et al., 2023) (Fig. 6, 7). This seasonal hydrological pattern has also been documented in studies from subtropical and Mediterranean climate regions (Brooks et al., 2010; Luo et al., 2019; Sprenger et al., 2019).

We also found that deep-rooted and shallow-rooted trees showed significant seasonal divergence in root zone water recharge (Fig. 6), which is consistent with the first hypothesis of this study. This difference mainly stems from the differences in the ability and pathways of the two to utilise different water sources, and the results of the electrical resistivity tomography (ERT) and the MixSIAR model together revealed the underlying hydrological mechanisms. The hydrological connectivity index of deep-rooted trees was lower than that of shallow-rooted trees during the rainy season with abundant precipitation (Fig. 6). The results from the MixSIAR model (Figure A1) indicate that rock fracture water is the primary source for all plants (contribution rate: 42.9%). However, deep-rooted trees can more readily access this water source (Schwinning, 2020; Querejeta et al., 2021; Liu et al., 2025a), which is supplemented by groundwater (contribution rate: 28%). This strategy makes their water sources less susceptible to interference from soil water affected by preferential flow. ERT profiles provide structural evidence for this: there is a significant low resistivity anomaly beneath deep-rooted trees, revealing their root system's use of deep water storage (Fig. 9). In contrast, the root systems of shallow-rooted trees are mostly distributed in the soil layer, and their second source of water is soil water (37% total contribution). Soil water retention attenuates the interference of preferential flow on water uptake (Xue et al., 2024), making it more susceptible to surface water dynamics, and thus exhibiting higher hydrological connectivity.

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During the dry season, the opposite pattern is observed: deep-rooted trees maintain higher hydrological connectivity. This is attributed to their ability to utilize deeper water sources (Cai et al., 2025b; Liu et al., 2024) and the advantage of reduced evaporation due to the reduction of litter cover, which prolongs the infiltration of precipitation (Li et al., 2024). The MixSIAR model further confirms that under water stress during the dry season, deep-rooted plants still rely on fissure water in rocks (Fig. A1). More importantly, the unique karst environment of the region creates conditions for deep-rooted plants to expand their underground "reservoirs". We believe that deep-rooted plants use the deep water storage mechanism through "root splitting" and the karst process to cope with drought, which also indirectly confirms the good water storage function of the epikarst zone. The continuous deep water supply capacity of this zone is the core mechanism for deep-rooted trees to maintain higher hydrological connectivity during the dry season (Fig. 9). These "reservoirs" mainly store rainwater through fissure channels during the rainy season and continuously supply water to the plants during the dry season. Therefore, when precipitation cannot effectively replenish the root zone, deep-rooted trees can turn to absorb these deeper "old water" with longer retention time (Zhao et al., 2024; Luo et al., 2023), while shallow-rooted trees face more severe water stress due to their difficulty in utilizing deep water sources.

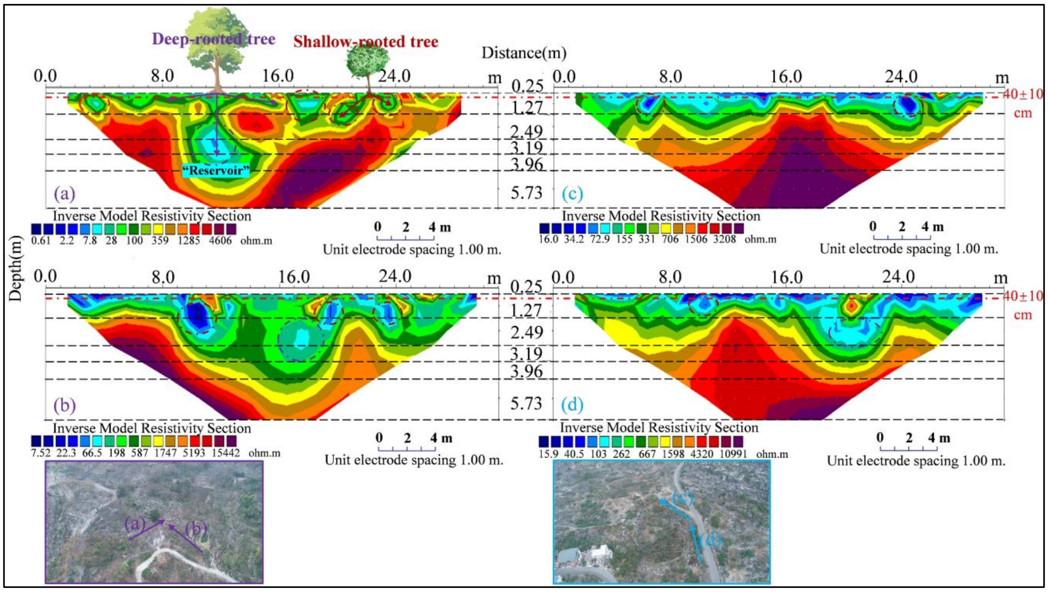

Fig. 9. shows the subsurface profiles of plant root zones obtained from Electrical Resistivity Tomography (ERT) inversion. The inverted electrical conductivity profiles were conducted at two sample plots. A total of four survey lines were deployed, each comprising 32 electrodes with a 1-meter spacing, achieving a subsurface investigation depth of approximately 6 meters (black dashed lines represent different investigation depths). (a) and (b) display the inversion results from one plot, while (c) and (d) show those from the other. Note: darker blue colors indicate lower electrical conductivity, corresponding to higher water content; arrows represent plant roots, purple dashed ellipses mark water storage zones associated with deep-rooted trees, and deep red dashed ellipses denote water storage zones associated with shallow-rooted trees. The red dashed line indicates the approximate soil depth (40 ± 10 cm) in the study area, revealing that most "water reservoirs" are located below the soil layer. These reservoirs store water during the rainy season and serve as a water source for deep-rooted trees during the dry season. The aerial photo was acquired by the authors using an unmanned aerial vehicle in December 2024.

4.2. The dominant role of root zone water supply dynamics in regulating transpiration water age

This study reveals that the root-zone water recharge rate (β) is the direct controller regulating the plant's transpiration water age (Fig. 7 and 8). Based on the principle of the piecewise linear mixing water age model, the transpiration water age is defined as the weighted average of the newly

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replenished water and the original water stored in the root zone: when the β value is high, the "new water" from recent precipitation dominates in the plant's water source, resulting in a younger water age (Luo et al., 2021); conversely, when the β value is low or zero, precipitation cannot effectively replenish the root-zone water (Brooks et al., 2010; Good et al., 2015; Luo et al., 2019), and the plant is forced to continuously utilize the "old water" with a longer retention time in the root zone (Barbeta et al., 2015; Barbeta and Peñuelas, 2017), causing the water age to significantly increase, which is in line with our second hypothesis. This mechanism clearly explains why the transpiration water age is generally lighter during the high recharge rate period in the rainy season, while it significantly ages during the low recharge rate period in the dry season (Fig. 4a, 6, 7).

The seasonal variations and interspecific differences in transpiration water age are fundamentally due to the difference in the age of water bodies that different depths of root systems come into contact with. However, in highly heterogeneous karst regions, accurately determining the depth of root distribution beneath hard rock layers remains a key and highly challenging task. To this end, through drilling exploration and endoscopic observation, the results show that plant roots are mainly distributed in the rock fissures within the depth range of 1.8 to 3.2 meters (Fig. A3), and a large number of fine roots were also observed in the rock fissures at the bottom of the exposed epikarst (with a thickness of approximately 3 meters) (Fig. A4). It should be noted that the depth of tree roots is affected by tree age and site conditions, which will be further explored in subsequent studies. Based on the latest research by Liu et al. (2025b), the water supplied in the 0-2 meter range is mainly recent recharge water, while the water in the >2 meter range is mainly "old water" that has been stored. We speculate that deep-rooted trees (rooting depth: 0–3.2 m or >3.2 m) can access both shallow "new water" and deep "old water," whereas shallow-rooted trees (rooting depth: 0–2 m) primarily rely on dynamic shallow sources. This is supported by ERT results, which indicate that the water reservoirs associated with deep-rooted trees are generally situated at greater depths than those of shallow-rooted trees (Figure 9). Consequently, deep-rooted trees consistently draw from reservoirs with a higher average water age. This directly explains their older transpiration water age compared to shallow-

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rooted trees across both wet and dry seasons (Fig. 7, 8), revealing a key mechanism by which root depth influences water source age.

Furthermore, in addition to root depth, plant water-use strategies can also influence root-zone water recharge and thus transpiration water age (Larcher, 2003). For example, 'water-efficient' plants effectively control transpiration losses through structural (e.g. leaf morphology) and physiological adaptations (e.g. stronger stomatal control), thus responding to soil drying and maintaining stable water potentials under wet and dry conditions (Tardieu and Simonneau, 1998). When confronted with water stress, this 'water-saving' strategy forces plants to obtain water from dry soil (Sprenger et al., 2019), resulting in an increase in plant transpiration water age. The most typical drought-tolerant plant in the study area is *Zanthoxylum bungeanum*, which was found to exhibit relatively smooth fluctuations in sap flow during the dry season (Fig. A2); whereas for taller trees, *Ailanthus altissima* and *Juglans regia*, they chose to "sacrifice" their leaves in order to maintain higher transpiration. Thus, water use strategy is an important ecological dimension that regulates the seasonal dynamics of transpiration water age by influencing the running time of plants.

4.3. Contributions, limitations and prospects of the study

This study reveals the ecohydrological mechanism of the "rock-root-water" synergy in the epikarst (Fig. 10). The rock fracture network, as the dominant hydrological pathway and key reservoir, influences the vertical distribution pattern of plant roots (Fig. A3, A4); the depth of the roots further determines the seasonal variation of the water replenishment rate (β) in the root zone. Based on the piecewise linear mixing water age model, the replenishment dynamics directly regulate the ratio of new and old water for plant water absorption. Ultimately, deep-rooted plants, due to their continuous utilization of the retained water in the deep fractures, have a significantly higher water age for transpiration in all seasons than shallow-rooted plants (Fig. 7, 8). This phenomenon is jointly verified by the deep water storage structure revealed by the high-density electrical method (Fig. 9, 10) and the water source analysis results of MixSIAR (Fig. A1). This mechanism clarifies the core role of the interaction between rocks and roots in regulating the temporal dimension of plant water utilization.

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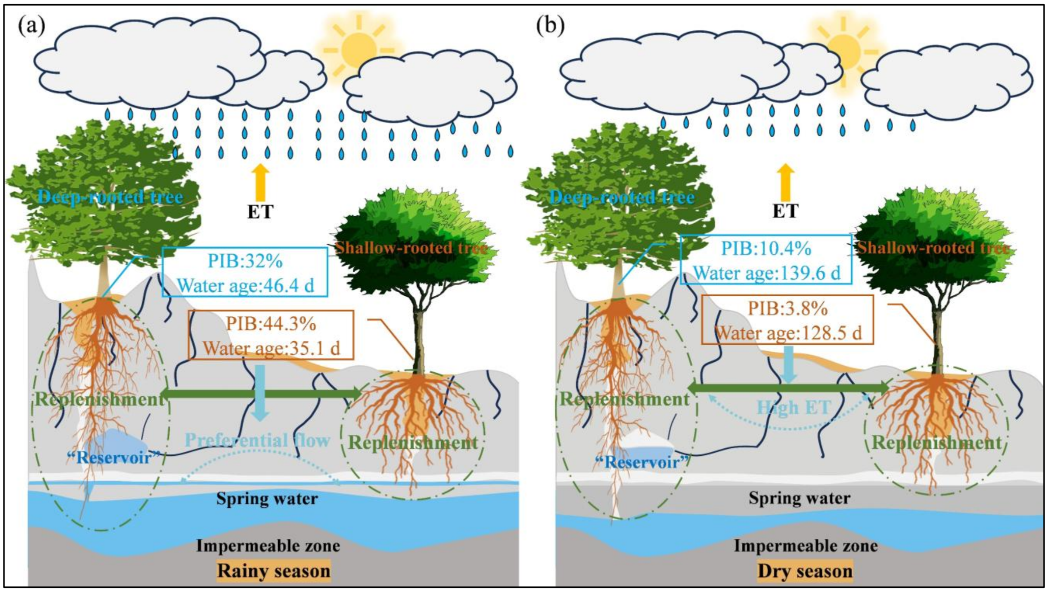

Fig. 10. Conceptual diagram of water recharge and transpiration age in the root zone of epikarst. (a) Frequent precipitation in the rainy season maintains high water recharge rates in the root zone of both deep-rooted and shallow-rooted trees, and the age of transpiration is rapidly updated; however, during heavy precipitation events, zero root zone recharge (β = 0%) can occur briefly due to preferential flow dominated by fissure ducts. (b) In the dry season, when precipitation is drastically reduced, plants generally turn to deep "old water" and transpiration ages are significantly higher; at the same time, low precipitation and high evapotranspiration combine to cause water to bypass the root zone (β = 0%). Transpiration ages were higher for deep-rooted trees than for shallow-rooted trees in all seasons due to the ability of deep-rooted trees to reach older water sources. Note: Yellow arrows indicate evapotranspiration (ET), light blue arrows are precipitation inputs, and green arrows indicate effective water recharge to the root zone; dark blue and orange boxes represent the root zone water recharge rate and transpiration age of deep-rooted versus shallow-rooted trees, respectively; PIB refers to plant root zone water recharge rate.

In the karst critical zone, the mechanism of plant transpiration water age formation is not dominated by the timing of physical transport of water through the vadose zone, but rather stems from the active selection of differently aged water reservoirs by the plant root system (Evaristo et al., 2015; Good et al., 2015; Luo et al., 2019; Brooks et al., 2010). Deep-rooted plants are able to directly reach and call upon deeply stored rock fissure water through a root system that extends into the rock fissure

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network (Schwinning, 2020; Querejeta et al., 2021); whereas shallow-rooted plants are only passively dependent on shallow, young, dynamic water sources due to limited root development (Luo et al., 2022). This ability to select water based on the ecological niche of the root system is fundamentally constrained by the interactions between the plant root system and the rock fracture network. While the rock fracture network provides water storage space and transport pathways, the depth of root distribution determines the accessibility of these water sources to plants, thus shaping distinct water age patterns.

It is noteworthy that mainstream research suggests long-term reliance on "old water" with extended residence times, while alleviating water stress in the short term, may increase ecosystem vulnerability (Roberts and Hanan et al., 2025; Liu et al., 2025). However, within the context of climate change—particularly in regions with limited water storage capacity like karst areas—this "old water" sustains transpiration during dry seasons, thereby creating a critical survival window for plants to await subsequent precipitation recharge. Therefore, this water utilization strategy can be regarded as an adaptive mechanism that enhances the drought-resistance resilience of plants and thereby improves the stability of the ecosystem.

However, there are still some limitations in this study. Firstly, the single-year observation period and limited sampling frequency may miss the short-term dynamic response of hydrological processes in the root zone, especially the rapid hydrological processes of precipitation pulse events in karst areas; secondly, the estimation of the root extent is too rough, and the dynamic mechanism of root development needs to be analysed in combination with the age of the tree and the site conditions in a systematic manner. In the future, we need to analyse the water transport mechanisms through artificial marker tracer experiments and high-frequency sampling, and focus on the dynamics of how precipitation infiltrates into the rock fissures and the subsurface, and is absorbed and utilised by plants (Sprenger and Allen, 2020), in order to deepen the understanding of ecohydrological processes.

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5. Conclusion

This study reveals the synergistic regulation mechanism between rock fissures and plant roots on the root zone water recharge process in karst epikarst and its profound effect on transpiration water age. Root depth was found to be a key factor regulating the seasonal dynamics of root zone water recharge: deep-rooted trees showed significantly lower recharge rates (32%) than shallow-rooted trees (44.3%) during the rainy season, whereas the opposite trend was observed during the dry season (10.4% for deep-rooted trees; 3.8% for shallow-rooted trees). This difference in recharge pattern further shaped the transpiration water age: deep-rooted trees had a higher water age (46.4 d) than shallow-rooted trees (35.1 d) during the rainy season, while the opposite was true during the dry season (deep-rooted trees: 139.6 d; shallow-rooted trees: 128.5 d). The results demonstrate that adopting a mixed-species configuration of deep- and shallow-rooted trees can establish complementary water-use strategies. This approach not only enhances the overall water-use efficiency of the system but also prevents the over-exploitation of deep water sources by any single deep-rooted species. It provides a crucial scientific basis for vegetation restoration and sustainable management in karst regions grounded in ecohydrological processes.

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Appendix A

Isotopic traceability analyses of xylem water, soil water at different depths, rock fissure water and spring water were carried out using the MixSIAR model. 0-20 cm was classified as shallow soil and 20-40 cm as deep soil.

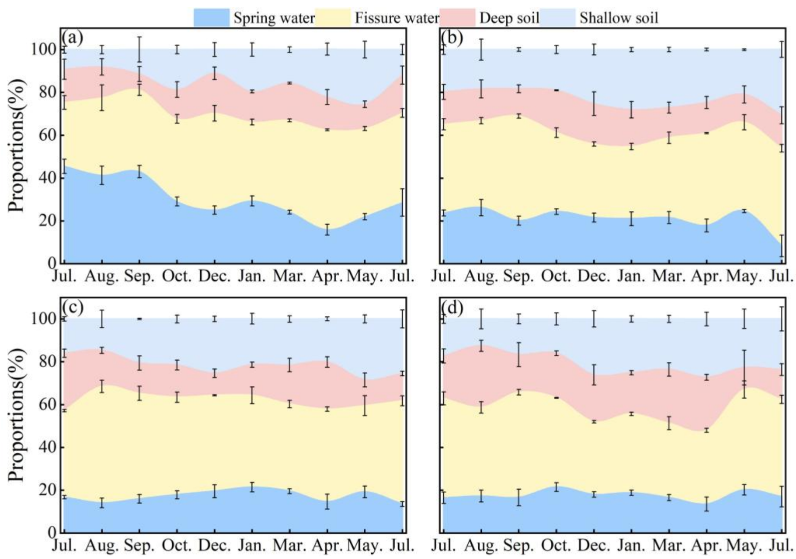

Fig. A1. Contribution of different water sources to plants. Where (a) is *Ailanthus altissima*, (b) is *Juglans regia*, (c) is *Zanthoxylum bungeanum*, (d) is *Eriobotrya japonica*.

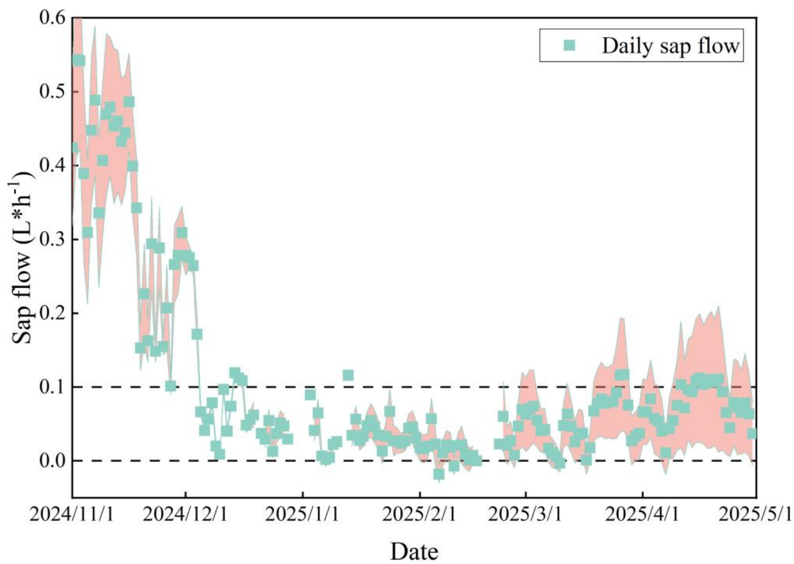

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Fig. A2. Variation in sap flow of *Zanthoxylum bungeanum* during the dry season hours during the study period. During November, the sap flow rate fluctuated significantly, which may be related to the large amount of residual precipitation recharge during the rainy season. After entering December, the sap flow rate dropped to a lower level of 0-0.1 L*h^{-1}, and the variation narrowed and stabilised. Note: Vacancies are due to instrument power failure due to prolonged rainy weather in the dry season, and shaded areas are standard deviations.

Fig. A3. Drilling process and root distribution in the surface karst zone. In order to explore the actual distribution depth of plant roots in the epikarst, we carried out a large number of borehole samples of arborvitae root systems along the mountain slopes. Through endoscopy, we found that the root system was densely distributed in the fissures, and the main distribution range was from 1.8 to 3.2 m in depth.

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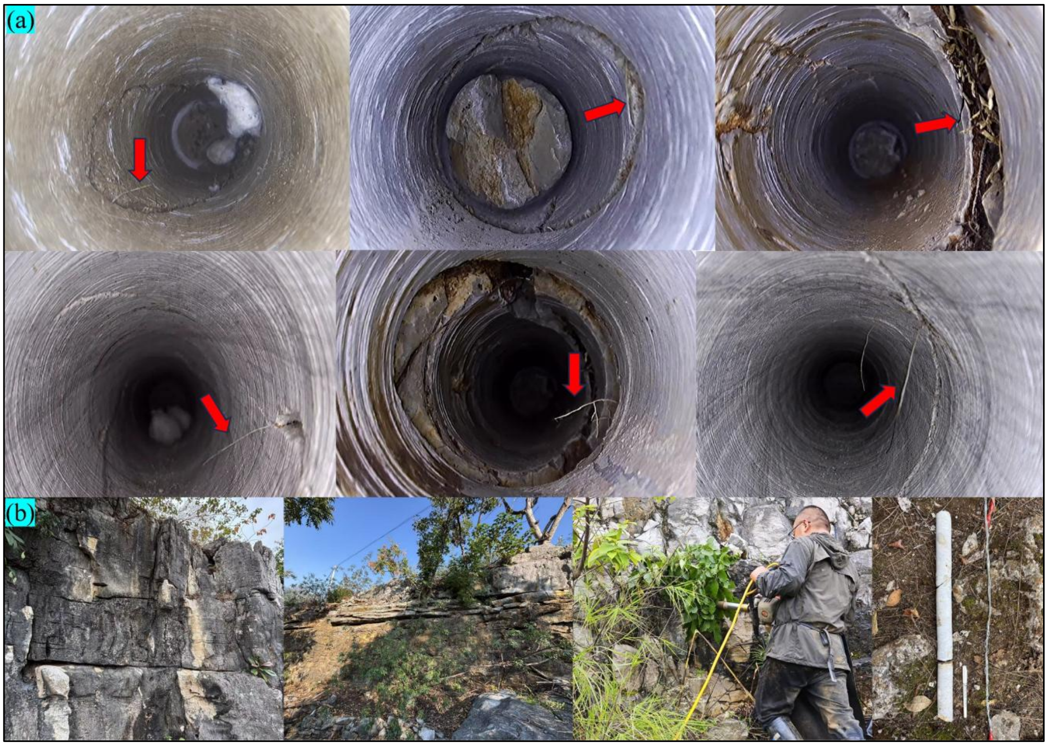

Fig. A4. Distribution of roots in rock fissure holes in exposed epikarst zones. We selected a number of epilithic karst zones with a thickness of more than 3 m to obtain rock fissure water by drilling diagonally downward from the base of the rock fissure (Fig. b). However, during the sampling period, we also detected the presence of a large number of roots within the holes (Fig. a).

Table A1 Summary of Plant Information for Plot Sites Detected by ERT

Species	Family	Life form	Leaf habit	DBH(cm)	Height(m)
Ailanthus altissima	Simaroubaceae	deep root	deciduous	47.8±2.75	11.8±0.8
Juglans regia	Juglandaceae	deep root	deciduous	25.8±2.95	6.9±0.8
Koelreuteria paniculata	Sapindaceae	deep root	deciduous	21.4±1.32	15.4±0.4
Zanthoxylum bungeanum	Rutaceae	shallow root	evergreen	3.8±0.88	2.5±0.5
Eriobotrya japonica	Rosaceae	shallow root	evergreen	8.4±0.35	3.4±0.4
Broussonetia papyrifera	Moraceae	shallow root	deciduous	5.7±0.23	4.1±0.2

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Data availability

The data collected in this study are available upon request to the authors. The data pertaining to this study can be found in the Mendeley Data repository, Version 1, doi: 10.17632/tvg3sj9m37.1

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Author contributions

Z: Writing – review & editing, Writing – original draft, Visualization, Software, Investigation, Formal analysis, Data curation, Conceptualization. L: Writing – review & editing, Supervision, Resources, Funding acquisition. Z: Writing – review & editing, Funding acquisition. L: Writing – review & editing, Resources, Methodology. C: Writing – review & editing. Z: Writing – review & editing, Supervision. L: Writing – review & editing, Investigation.

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