

## Plant water resource partitioning and xylem-to-leaf deuterium enrichment in Lanzhou, northwest China

Qinqin Du, Mingjun Zhang, Shengjie Wang, Athanassios A. Argiriou, Cunwei Che, Peipei Zhao, Zhuanzhuan Ma and Pengyan Su

### ABSTRACT

Lanzhou lies at the western Loess Plateau, China, and has a typical semi-arid temperate continental climate. Plants in this area are exposed to a prolonged dry season. In this study, we measured the stable isotopes of hydrogen ( $\delta D$ ) and oxygen ( $\delta^{18}O$ ) of the local precipitation, river water, soil water, plant xylem water, and leaf water at four sampling sites during the 2016 growing season. Our results showed that plants relied mostly on wet season precipitation at sites N1, N2, and N3 because this recharged the soil after the long dry season. Leaf phenology had a significant effect on evaporation distance (ED) value, and evergreen plants have adapted to water tapping from deep soil water sources during the dry season. The ED values of trees and shrubs were quite different in the dry season, indicating water competition among different plant species was mitigated due to water resource partitioning. Moreover, plants at site N4 relied on a water source admixed with river water throughout the whole growing season. The mean value of xylem-to-leaf water deuterium enrichment ( $\epsilon_{l/x}$ ) was  $-0.91 \pm 0.36\%$  over all plant species, seasons, and sampling sites. Plant species, leaf phenology, and seasons were found to be the primary factors influencing the  $\epsilon_{l/x}$ , while growth form and elevation had negligible effects.

**Key words** | deuterium enrichment, Lanzhou, plant, stable isotope, water resource partitioning

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### INTRODUCTION

Plants are an important component of the regional water cycles, controlling 50–90% of the evapotranspiration of an ecosystem (Yaseef *et al.* 2010; Coenders-Gerrits *et al.* 2014). In arid and semi-arid regions, water is the primary limiting factor affecting the establishment and survival of plants, and interspecific (below ground) competition for water defines plant communities (Schenk & Jackson 2002). Plants must cope with water shortages during their life cycles (Palacio *et al.* 2017). There is evidence that different species can coexist by using different ranges and proportions of resources (Filella & Peñuelas 2003; Wang *et al.* 2019), such as the use of water-source segregation between growth forms in several environments (Barbeta & Peñuelas 2017). It has

been proposed that trees strongly compete with shrubs for the same water resources (Schnitzer & Bongers 2011). Plant water-use patterns reflect the complex interactions between different functional types and environment conditions. Therefore, knowledge of the processes underlying plant water resource partitioning is critical for understanding soil–plant interactions and evaluating plant adaptability in water-limited ecosystems.

The analysis of stable hydrogen and oxygen isotope ratios ( $\delta D$  and  $\delta^{18}O$ ) is an effective and powerful approach for investigating plant water resource partitioning (Dawson & Ehleringer 1991; Evaristo & McDonnell 2017). Water uptake from the roots and its transportation through the

plant stem is generally considered to occur without fractionation (Stratton *et al.* 2000), except for some mangrove and halophytic species (Lin & Sternber 1993). In so doing, the isotopic composition of xylem water of plants represents the composition of water sources (Asbjornsen *et al.* 2007). More field-based plant water studies have shown that plants rarely access rainfall directly and use mostly resident, stored soil pore water (Brooks *et al.* 2010; Goldsmith *et al.* 2011; Hervé-Fernández *et al.* 2016). Soil water isotopic composition is spatially heterogeneous and highly variable (Goldsmith *et al.* 2018). Thus, explicitly accessing temporal and spatial variations in the stable isotopes of water and plant water uptake is important to improve understanding of the mechanisms behind plant water resource partitioning. Recent investigations have also shown that enhanced temporal and spatial sampling resolution of stable isotopes of  $\delta\text{D}$  and  $\delta^{18}\text{O}$  is key to improved understanding of plant water-use patterns (Goldsmith *et al.* 2018; Allen *et al.* 2019; Sprenger *et al.* 2019).

Due to transpiration, the isotopic composition of leaf water differs markedly from that of xylem water because the lighter isotopologues of water diffuse more readily than the heavier ones (Barbour *et al.* 2017). Unraveling the complete pathway of water entering a vegetated catchment as precipitation, traveling through soil, and eventually leaving the system either as stream water or as water vapor from plants and bare surfaces is crucial to understanding the regional water cycles (Sohel *et al.* 2019). Therefore, the transpiration processes from xylem-to-leaf water with isotopic enrichment is one of the important components. The drier and warmer the ambient atmosphere, and the windier local weather conditions, the larger the rate of transpiration will be and thus the required rate of water uptake (Jackson *et al.* 1995). As regulators of the ecophysiological performance of individual plants, the relative humidity and air temperature are critical environmental parameters for water and carbon cycling at the ecosystem scale (Kahmen *et al.* 2011). Some studies also show that air temperature, relative humidity- and isotopic composition of water vapor surrounding the plant mainly determine the isotopic enrichment from the xylem to the leaf water (Kahmen *et al.* 2013). Therefore, it is necessary to understand how the physiological, morphological- and environmental factors affect leaf water enrichment in heavy isotopes during plant

transpiration, which is important for many physiological, ecological, and paleoclimate researches (Holloway-Phillips *et al.* 2016). However, to our knowledge, no studies have been conducted to explore the xylem-to-leaf water deuterium enrichment in urban ecosystems in arid and semi-arid areas of China.

Lanzhou is the capital of Gansu Province and is located in the semi-arid northwest China, which has a typical semi-arid temperate continental climate. The city also lies at the transitional zone between monsoon climate zone and non-monsoon climate zone, and the Yellow River, which passes through the inner city from west to east, has formed a special ecological environment. The city is representative of arid and semi-arid urban ecosystems, with sparse vegetation and limited precipitation. The vegetation of this area has dramatically changed in recent years (Chen *et al.* 2019). Despite this, little is known about the temporal and spatial variations in water resource partitioning of the main plant species that inhabit this region, and plant adaptability and hydrogen isotopic fractionation from xylem to leaf water in this region remain poorly understood. In this study, we therefore measured the  $\delta\text{D}$  and  $\delta^{18}\text{O}$  of precipitation, river water, soil water, and plant xylem and leaf water in two plant members of each of the eight plant species at four sampling sites with different elevations around Lanzhou. Our primary research aims were to determine the temporal and spatial variations of plant water resource partitioning in Lanzhou and to explore the influence that these environmental drivers have on the leaf-water isotopic fractionation associated with evaporation at each of Lanzhou's sampling sites. This study can provide a basis for the study in water resource partitioning of plants in arid and semi-arid urban ecosystems.

## MATERIALS AND METHODS

### Study area

This study was conducted in Lanzhou, which is located in the upper reaches of the Yellow River and the geometric center of China's land territory. The city is encircled by mountains, with a mean elevation of 1,500 m. According to the long-term climatology from 1981 to 2010, the mean

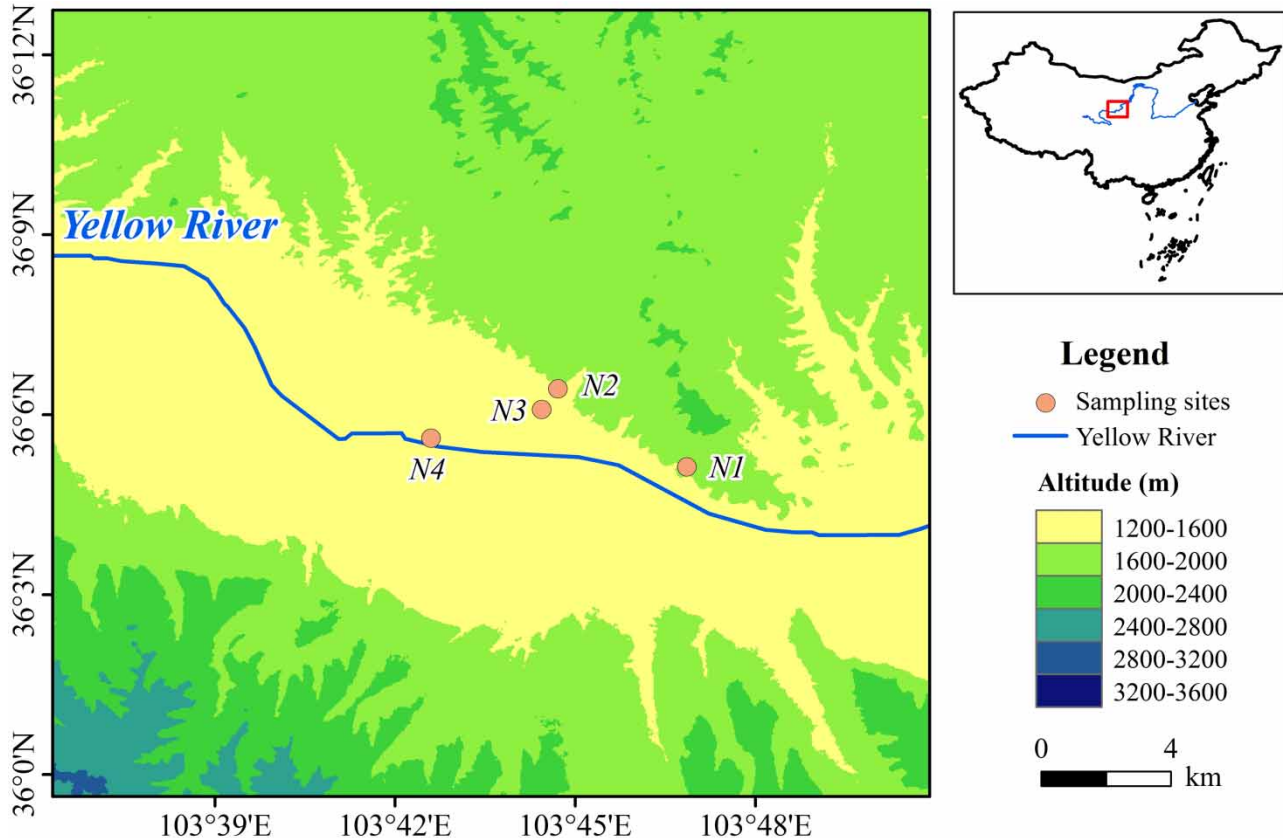
annual air temperature is 10.4 °C, ranging from −4.5 °C in January to 23.1 °C in July. The annual precipitation amount is less than 400 mm because the area is located deep in the mainland, far from the surrounding oceans, and precipitation occurs mostly during summer (Chen et al. 2015).

### Sample collection

Lanzhou is a typical valley city with obvious elevation gradient. We assume that elevation has a significant influence on the plant survival and growth; therefore, according to the principle of elevation gradient, the four sites, Jiuzhoutai (N1: 103.78°E, 36.09°N, 2,054 m), Beishan (N2: 103.73°E, 36.11°N, 1,667 m), the Northwest Normal University (N3: 103.73°E, 36.10°N, 1,553 m), and Wetland park (N4: 103.72°E, 36.08°N, 1,509 m) were located north of the Yellow River and selected as the sampling sites (Figure 1). The changes in elevation show that:  $N1 > N2 > N3 > N4$ .

The site N4 is very close to the Yellow River. Eight typical plant species with varying growth form (tree, shrub, or herb) and leaf phenology (evergreen or deciduous) were collected in the four sampling sites (Table 1). Shrubs were defined as woody plants with multiple stems, while trees had one erect perennial stem.

From April to October 2016 (growing season), river water, soil, and plant xylem and leaf samples were collected once a month, precipitation samples were collected on a per event basis. Sampling was performed as follows. (1) plant xylem and leaf samples: plant samples were collected between 08:00 and 11:00 a.m. to minimize the influence of external factors, such as illumination, on the results of isotopic analysis. Two plants of the same species with good growth and high consistency were selected. From each plant, five to seven bolted branches were cut, with diameters of about 0.3 cm and lengths of about 5 cm. After peeling off the epidermis quickly, the bolted branches were put into 10-mL glass vials with threaded opening and sealed with Parafilm sealing film



**Figure 1** | Spatial distribution of the sampling sites in Lanzhou.

**Table 1** | Studied plant species and their respective family, growth form, leaf phenology, and location

Species	Family	Growth form	Leaf phenology	Location
<i>Platyclusus orientalis</i>	Cupressaceae	Tree	Evergreen	N1, N2
<i>Sophora japonica</i>	Leguminosae	Tree	Deciduous	N3, N4
<i>Salix babylonica</i>	Salicaceae	Tree	Deciduous	N3, N4
<i>Caragana korshinskii</i>	Leguminosae	Shrub	Deciduous	N1, N2
<i>Rosa xanthina</i>	Rosaceae	Shrub	Deciduous	N3, N4
<i>Agropyron cristatum</i>	Gramineae	herb	Perennial	N1, N2
<i>Medicago</i>	Gramineae	herb	Perennial	N3, N4
<i>Phragmites communis</i>	Gramineae	herb	Perennial	N4

in order to be transported to the laboratory where the samples continued to be kept in the cooler until the water was quantitatively extracted (Wu et al. 2016). If twigs were sampled, the leaves on those twigs were also sampled. (2) Soil samples were collected simultaneously with plant tissues, in the proximity of the sampled plants, using a hand auger. Soil samples were taken from the surface and up to a depth of 100 cm, at 10-cm intervals, which were divided into two: one subsample was immediately packed into 10-mL glass vials with threads sealed with a screw-lid and Parafilm wrap and placed in a cooler where it was refrigerated until water extraction for isotopic analysis; the other subsample was sealed in an aluminum box and placed into a cooler for measuring soil water content (SWC, %). (3) Event-based precipitation samples were collected using a 300-mL rain gauge near the site N3 where neither trees nor buildings were present. The samples were immediately bottled in plastic bottles, wrapped in Parafilm and refrigerated at 2 °C until their analysis. A total of 35 precipitation samples were collected during the growth season. In addition, the meteorological parameters (precipitation amount and air temperature) were recorded by a weather station near site N3. (4) Monthly river water samples were collected from the Yellow River, near site N4.

### Laboratory analysis

The soil, plant xylem, and leaf water were extracted using a cryogenic vacuum distillation system (LI-2000 Automatic Vacuum Condensation Extraction System). The stable hydrogen and oxygen isotopic composition of all liquid

samples, including precipitation and river water, were analyzed using a liquid water isotope analyzer (DLT-100, Los Gatos Research, USA) at the Stable Isotope Laboratory, College of Geography and Environmental Science, Northwest Normal University. The measurement uncertainties in this study for  $\delta D$  and  $\delta^{18}O$  are  $\pm 0.60\text{‰}$  and  $\pm 0.20\text{‰}$ , respectively. The measured  $\delta D$  and  $\delta^{18}O$  values were expressed as per millesimal unit with respect to the Vienna Standard Mean Ocean Water (VSMOW):

$$\delta = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1,000\text{‰} \quad (1)$$

where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  represent the molar abundance ratios ( $^{18}O/^{16}O$ ,  $^2H/^1H$ ) of the sample and of the standard, respectively.

The monthly amount-weighted mean of  $\delta D$  and  $\delta^{18}O$  for precipitation was calculated as follows:

$$\delta \bar{P} = \frac{\sum_i^n \delta_i \times PPT_i}{\sum_i^n PPT_i} \quad (2)$$

where  $\delta_i$  and  $PPT_i$  represent the isotopic content of an event-based precipitation and the event-based precipitation amount, respectively.

### Data analysis

In this study, seasonal characterization was performed as follows: samples collected from June to September were attributed to the wet season and those collected from October to May to the dry season. Since the SWC and isotopic composition of soil water varied significantly along the entire soil profile, three potential soil water source layers (0–30 cm, 30–60 cm, and 60–100 cm) were defined for the needs of this analysis (Wu et al. 2016) as follows:

- (1) Shallow soil layer (0–30 cm): SWC and soil water isotopic composition varied significantly and were sensitive to precipitation pulse input and evaporation depending on the season and depth.
- (2) Middle soil layer (30–60 cm): lower soil water isotopic composition and milder monthly changes than in the shallow soil layer.

- (3) Deep soil layer (60–100 cm): relatively stable variations in isotopic composition of soil water and SWC through the entire soil profile.

The  $\delta D$  values of plant xylem and leaves ( $\delta D_{\text{xylem}}$  and  $\delta D_{\text{leaf}}$ ) were used to calculate the enrichment factor ( $\epsilon_{1/x}$ ) characterizing the hydrogen isotopic fractionation from xylem to leaf water (Kahmen *et al.* 2013) as follows:

$$\epsilon_{1/x} = \frac{\delta D_{\text{leaf}} + 1}{\delta D_{\text{xylem}} + 1} - 1 \quad (3)$$

Since the local meteoric water line (LMWL) describes the meteoric water inputs to the catchment,  $\delta^{18}\text{O}_{\text{LMWL-int}}$  and  $\delta D_{\text{LMWL-int}}$  (to be read as the stable isotope LMWL intersection) were calculated to trace the isotopic signature of the precipitation source for the water compartments measured in this study (i.e. xylem water). The average isotopic signature of the source of xylem water was determined from the intersection of xylem water samples (aligned along a local evaporation line, LEL) with the LMWL. Calculations were made following Hervé-Fernández *et al.* (2016):

$$\delta^{18}\text{O}_{\text{LMWL-int}} = \frac{\delta D - \text{slope}_{\text{LEL}} \times \delta^{18}\text{O} - \text{intercept}_{\text{LMWL}}}{\text{slope}_{\text{LMWL}} - \text{slope}_{\text{LEL}}} \quad (4)$$

$$\delta D_{\text{LMWL-int}} = \delta^{18}\text{O}_{\text{LMWL-int}} \times \text{slope}_{\text{LMWL}} + \text{intercept}_{\text{LMWL}} \quad (5)$$

The hydrogen isotopic signatures of xylem samples follow an evaporation line (LEL), and  $\text{slope}_{\text{LEL}}$  represents

the slope of LEL. The  $\text{slope}_{\text{LMWL}}$  and  $\text{intercept}_{\text{LMWL}}$  represent the slope and intercept of LMWL, respectively.

The isotopic signatures of xylem water were further characterized with a parameter describing the relative degree of evaporation, termed as evaporation distance (ED). This is defined as the distance from the LMWL along an evaporation line, scaled to the  $\delta D$  axis (Equation (6)) as follows:

$$\text{ED} = \sqrt{(\delta D - \delta D_{\text{LMWL-int}})^2 + \text{slope}_{\text{LMWL}} \times (\delta^{18}\text{O} - \delta^{18}\text{O}_{\text{LMWL-int}})^2} \quad (6)$$

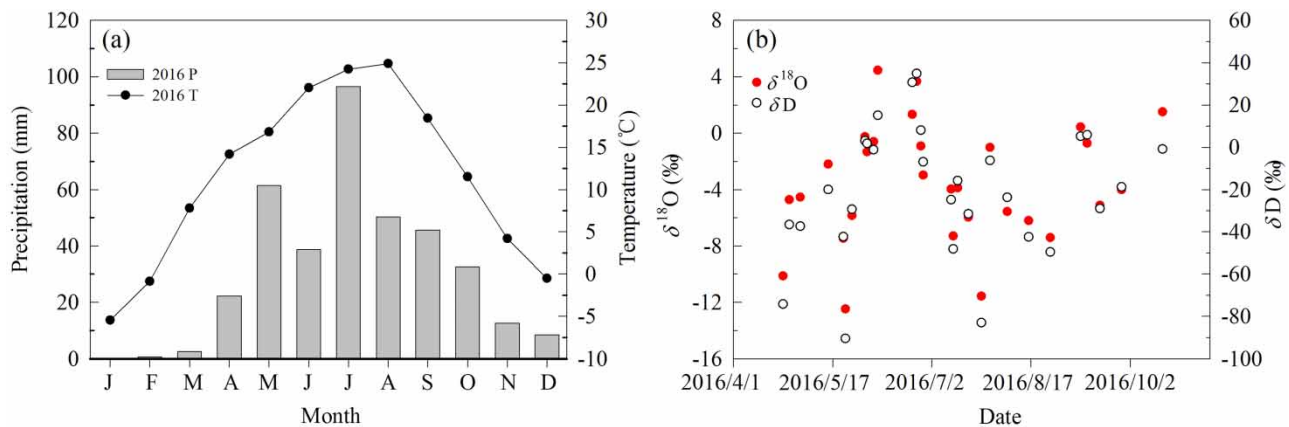
The higher this ED value, the further away from the LMWL and the more evaporated the water will be, i.e. the concentration of heavy isotopes will be higher.

Slopes and intercepts of the LMWL and LELs were calculated using linear regression. To explore the different sources of plant water use, a discussion about the different slopes and intercepts is provided in this paper.

## RESULTS

### Isotopic signatures of precipitation, river water, and soil water

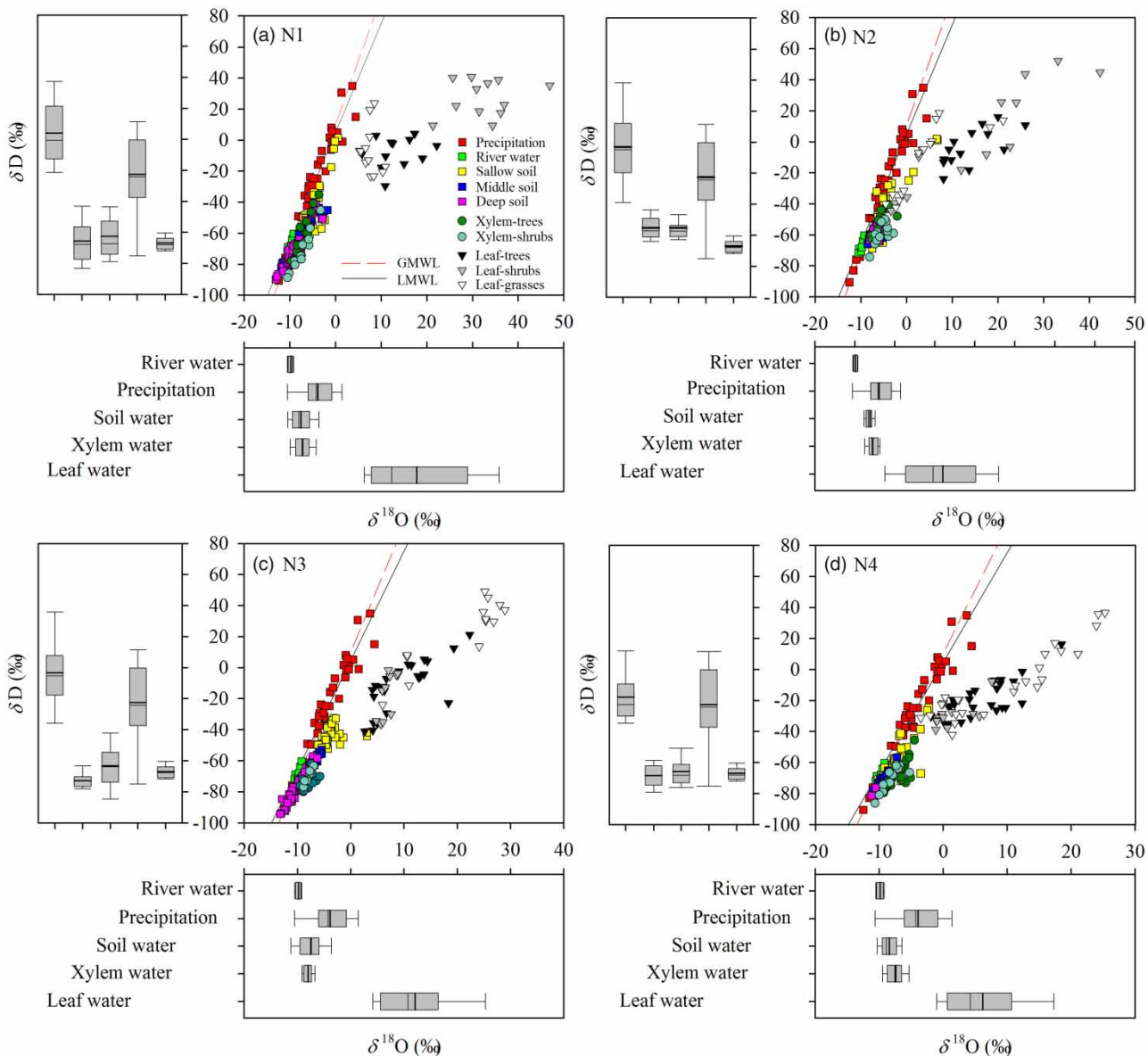
During this study (2016), the monthly average air temperature ranged from  $-12.9^\circ\text{C}$  to  $29.8^\circ\text{C}$  (annual mean value:  $11.4 \pm 10^\circ\text{C}$ ), where the air temperature maximum ( $24.2^\circ\text{C}$ ) occurred in July and the minimum ( $-5.4^\circ\text{C}$ ) in January (Figure 2(a)). The total amount of



**Figure 2** | Variations of mean precipitation amount, air temperature, and isotopic composition in precipitation: (a) the monthly variation of air temperature and precipitation amount in 2016; and (b) the temporal variation of isotopic compositions in precipitation during the 2016 growing season.

local precipitation was 372 mm, of which 66.5% (231.3 mm) occurred in the wet season and 33.5% (116.4 mm) in the dry season. The event-based isotopic composition of precipitation ( $\delta D_{\text{prec}}$  and  $\delta^{18}\text{O}_{\text{prec}}$ ) varied significantly within the plant growing season (Figure 2(b)). The  $\delta D_{\text{prec}}$  and  $\delta^{18}\text{O}_{\text{prec}}$  ranged from  $-90.52\text{‰}$  to  $34.82\text{‰}$  and  $-12.48\text{‰}$  to  $4.44\text{‰}$ , respectively, with monthly amount-weighted values of  $-39.3\text{‰}$  and  $-6.31\text{‰}$ , respectively. The isotopic

values of precipitation were most enriched during the wet season of June, with values of  $10.09\text{‰}$  for  $\delta D_{\text{prec}}$  and  $0.37\text{‰}$  for  $\delta^{18}\text{O}_{\text{prec}}$ , and most depleted during the dry season of April, with values of  $-55.46\text{‰}$  for  $\delta D_{\text{prec}}$  and  $-7.43\text{‰}$  for  $\delta^{18}\text{O}_{\text{prec}}$ , respectively. The LMWL ( $\delta D = 7.08 \delta^{18}\text{O} + 5.12$ ,  $n = 35$ ) in Figure 3 had a slightly lower slope and about half the intercept value compared with the global meteoric water line (GMWL:  $\delta D = 8.1 \delta^{18}\text{O} + 10.3$



**Figure 3** | The  $\delta D$  and  $\delta^{18}\text{O}$  values of precipitation, river water, soil water, xylem water, and leaf water of all plant species across different seasons and sampling sites. Dotted line represents LMWL and solid line represents GMWL. The boxplots showed the mean (bold line), minimum, first quartile, median, third quartile, and maximum for the isotopic compositions of leaf water, xylem water, precipitation, river water, and soil water.

(Rozanski *et al.* 1993)), indicating that an apparent evaporation enrichment occurred in our study area.

The isotopic compositions of river water revealed very little seasonal variations in  $\delta D$  ( $\delta D_{\text{river}}$ ) and  $\delta^{18}O$  ( $\delta^{18}O_{\text{river}}$ ), mainly concentrated near the LMWL (Figure 3). The mean  $\delta D_{\text{river}}$  (ranging from  $-71.90\text{‰}$  to  $-60.31\text{‰}$ ) and  $\delta^{18}O_{\text{river}}$  (ranging from  $-10.52\text{‰}$  to  $-9.20\text{‰}$ ) value were  $-66.83 \pm 4.18\text{‰}$  and  $-9.81 \pm 0.71\text{‰}$  during seven consecutive months, respectively (Table 2). The soil water isotopic values were generally distributed along and below the right of the LMWL, which suggested that soil water had undergone evaporation enrichment, especially in shallow soil layer.

### Isotopic composition of xylem water

At the four sampling sites, the dual isotopic signature of xylem water, leaf water, soil water, and river water were plotted along the LMWL (Figure 3). The  $\delta D$  of xylem water ( $\delta D_{\text{xylem}}$ ) in a total of 117 analyzed samples (no

grasses) had an overall mean value of  $-65.67 \pm 11.12\text{‰}$  (ranging from  $-88.67\text{‰}$  to  $-35.29\text{‰}$ ) across all plants during sampling period, and  $\delta^{18}O$  of xylem water ( $\delta^{18}O_{\text{xylem}}$ ) ranged from  $-10.66\text{‰}$  to  $5.68\text{‰}$  with an average of  $-6.90 \pm 2.35\text{‰}$ . The variations of  $\delta D_{\text{xylem}}$  showed that N2 ( $-55.23 \pm 8.14\text{‰}$ ) > N1 ( $-65.56 \pm 14.22\text{‰}$ ) > N4 ( $-68.31 \pm 8.28\text{‰}$ ) > N3 ( $-72.90 \pm 4.96\text{‰}$ ). At sites N1 and N4, the  $\delta D_{\text{xylem}}$  and  $\delta^{18}O_{\text{xylem}}$  values of trees were higher than the shrubs, but no obvious differences of isotopic values were observed between the trees and shrubs at sites N2 and N3. Across all sampled plants, leaf phenology (deciduous or evergreen) had significant influence on the  $\delta D_{\text{xylem}}$  value. In terms of different seasons (Table 2), the  $\delta^{18}O_{\text{xylem}}$  and  $\delta D_{\text{xylem}}$  of trees or shrubs showed no significant seasonality across the four sampling sites.

An evaporation line (LEL:  $\delta D = 5.31 \times \delta^{18}O - 28.11$ ;  $n = 117$ ) was obtained from all xylem samples, with a slope and intercept lower than those of LMWL. LELs across four sampling sites were used to calculate  $\delta D_{\text{LMWL-int}}$ . It was

**Table 2** | The average  $\delta^{18}O$  (‰) and  $\delta D$  (‰) value (mean  $\pm$  SD) for precipitation, shallow, middle, deep soil water, river water, and xylem water for trees and shrubs plantation at four sampling sites across different seasons

Sample	Sites	$\delta^{18}O$ (‰)		$\delta D$ (‰)	
		Wet season	Dry season	Wet season	Dry season
Precipitation		$-3.25 \pm 3.97$	$-5.36 \pm 4.32$	$-16.53 \pm 29.02$	$-37.09 \pm 29.16$
River water		$-9.50 \pm 0.31$	$-10.22 \pm 0.41$	$-64.77 \pm 4.36$	$-69.57 \pm 2.07$
Shallow soil	N1	$-5.33 \pm 1.88$	$-6.26 \pm 2.68$	$-44.08 \pm 19.80$	$-58.28 \pm 16.22$
	N2	$-4.33 \pm 4.10$	$-6.02 \pm 1.41$	$-44.50 \pm 17.97$	$-53.12 \pm 14.66$
	N3	$-5.04 \pm 2.53$	$-3.27 \pm 2.66$	$-48.86 \pm 11.99$	$-45.68 \pm 5.18$
	N4	$-7.47 \pm 2.34$	$-7.02 \pm 1.15$	$-58.80 \pm 13.99$	$-59.00 \pm 8.59$
Middle soil	N1	$-8.45 \pm 1.88$	$-6.40 \pm 2.38$	$-67.82 \pm 9.29$	$-63.67 \pm 13.78$
	N2	$-7.01 \pm 1.00$	$-6.87 \pm 0.83$	$-59.71 \pm 4.09$	$-58.77 \pm 4.18$
	N3	$-8.17 \pm 1.38$	$-7.15 \pm 1.02$	$-67.08 \pm 8.67$	$-66.96 \pm 7.87$
	N4	$-9.47 \pm 0.73$	$-9.01 \pm 0.73$	$-72.15 \pm 3.17$	$-69.84 \pm 5.55$
Deep soil	N1	$-10.37 \pm 1.75$	$-8.98 \pm 1.44$	$-75.19 \pm 6.88$	$-64.01 \pm 13.00$
	N2	$-6.50 \pm 0.94$	$-6.55 \pm 0.40$	$-55.87 \pm 3.55$	$-57.80 \pm 2.75$
	N3	$-9.88 \pm 1.46$	$-7.81 \pm 2.26$	$-77.99 \pm 9.58$	$-71.81 \pm 9.08$
	N4	$-10.82 \pm 0.48$	$-10.27 \pm 0.70$	$-78.81 \pm 3.58$	$-77.87 \pm 2.87$
Xylem trees	N1	$-6.27 \pm 1.24$	$-7.60 \pm 2.22$	$-54.66 \pm 9.88$	$-64.17 \pm 16.28$
	N2	$-5.73 \pm 1.27$	$-5.25 \pm 1.90$	$-50.39 \pm 8.28$	$-52.16 \pm 7.83$
	N3	$-8.31 \pm 1.03$	$-7.48 \pm 0.8$	$-74.05 \pm 4.84$	$-72.95 \pm 5.46$
	N4	$-7.32 \pm 1.50$	$-7.00 \pm 1.42$	$-66.26 \pm 9.14$	$-69.13 \pm 6.67$
Xylem shrubs	N1	$-7.33 \pm 1.44$	$-7.45 \pm 2.72$	$-70.30 \pm 9.05$	$-73.11 \pm 15.65$
	N2	$-5.87 \pm 1.39$	$-4.90 \pm 1.46$	$-58.43 \pm 8.36$	$-60.50 \pm 2.11$
	N3	$-7.93 \pm 0.82$	$-8.14 \pm 0.51$	$-70.14 \pm 6.15$	$-71.43 \pm 2.37$
	N4	$-8.63 \pm 1.45$	$-7.22 \pm 1.39$	$-72.61 \pm 9.38$	$-67.31 \pm 2.52$

found that the  $\delta D_{LMWL-int}$  (mean value:  $-98.23 \pm 17\text{‰}$ ) ranged from  $-146.22\text{‰}$  to  $-57.91\text{‰}$  for all plant samples. Comparing the results between the four sites (Figure 4), the  $\delta D_{LMWL-int}$  decreased as follows: N2 (mean value:  $-88.26 \pm 19\text{‰}$ ) > N1 (mean value:  $-96.15 \pm 20\text{‰}$ ) > N4 (mean value:  $-102.00 \pm 16\text{‰}$ ) > N3 (mean value:  $-105.47 \pm 11\text{‰}$ ), indicating that the higher the elevation, the greater the  $\delta D_{LMWL-int}$  value. The plants at the four sites showed negative  $\delta D_{LMWL-int}$  values in the dry season, which was consistent with the lower isotope values of precipitation during the dry season. The lowest  $\delta D_{LMWL-int}$  value at all sites was observed in April and the highest in September.

In this study, the ED values across all plant samples ranged from  $11\text{‰}$  to  $136\text{‰}$  (mean value:  $38.04 \pm 16.15\text{‰}$ ) (Figure 4). The plants from site N4 showed systematically higher ED values (mean value:  $41.6 \pm 23.84\text{‰}$ ) than those from site N3 (mean value:  $38.33 \pm 9.95\text{‰}$ ), N2 (mean value:  $38.04 \pm 16.15\text{‰}$ ), and N1 (mean value:  $36 \pm 11.38\text{‰}$ ). The ED values decreased in the sense N4 > N3 > N2 > N1, i.e. the higher the elevation, the lower the ED value. The ED value at site N4 was highest because plants from this site used a substantial fraction of the Yellow River water, which had relatively enriched  $\delta D_{river}$ . The ED value

was maximum at all sampling sites during the dry season, especially in April, and minimum during the wet season.

### Leaf water and factor ( $\epsilon_{l/x}$ ) of xylem-to-leaf deuterium enrichment

A total of 201 plant samples were collected to analyze leaf water  $\delta D$  ( $\delta D_{leaf}$ ) and  $\delta^{18}O$  ( $\delta^{18}O_{leaf}$ ) variations during the growing season, including three species of grasses (*Agropyron cristatum*, *Medicago*, *Phragmites australis*). The isotopic compositions of leaf water varied obviously among plant species, sampling sites, and seasons. The  $\delta D_{leaf}$  ranged from  $-64.52\text{‰}$  to  $59.35\text{‰}$  (mean value:  $-6.05 \pm 23.26\text{‰}$ ) across all samples (Figure 4), and  $\delta^{18}O_{leaf}$  ranged from  $-7.67\text{‰}$  to  $51.42\text{‰}$  (mean value:  $11.06 \pm 10.52\text{‰}$ ). In relation to the growth form of plants, the  $\delta D_{leaf}$  of trees (mean value:  $-11.61 \pm 14.31\text{‰}$ ) were less enriched than those of shrubs (mean value:  $-1.31 \pm 29.90\text{‰}$ ), while grasses were intermediate (mean value:  $-2.88 \pm 25.26\text{‰}$ ).

The deuterium enrichment factor ( $\epsilon_{l/x}$ ) of xylem-to-leaf water was calculated based on 117 pairs of  $\delta D_{xylem}$  and  $\delta D_{leaf}$  values (Figure 5). The  $\epsilon_{l/x}$  for  $\delta^{18}O$  was not discussed here because it follows the same trend as the  $\delta D$ . Our results

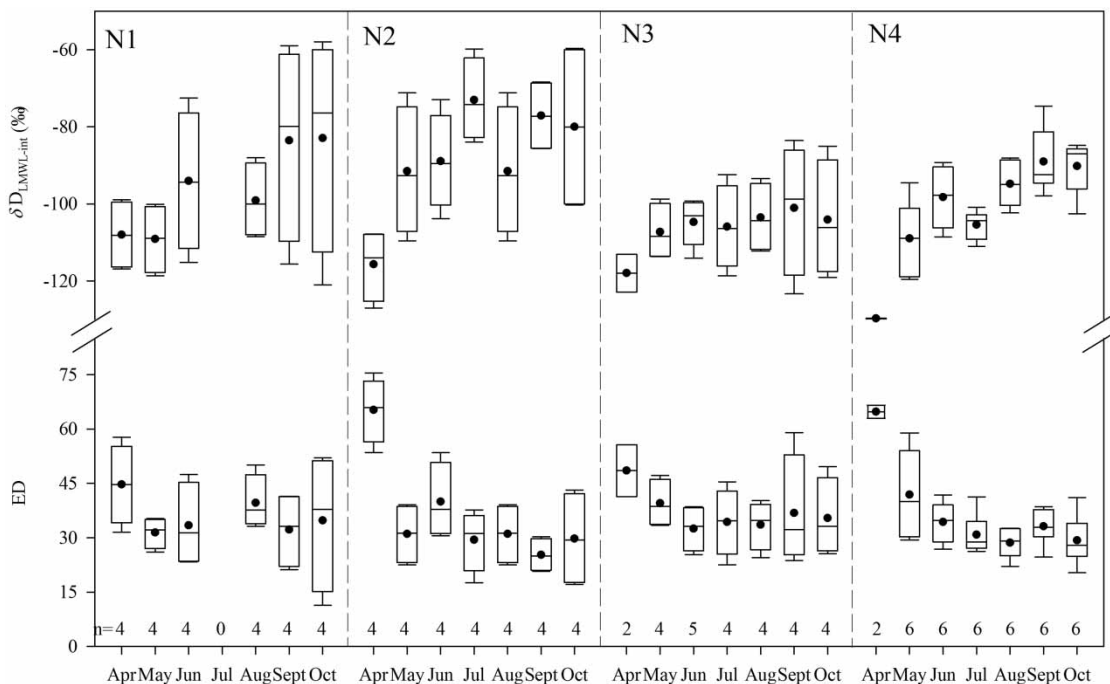
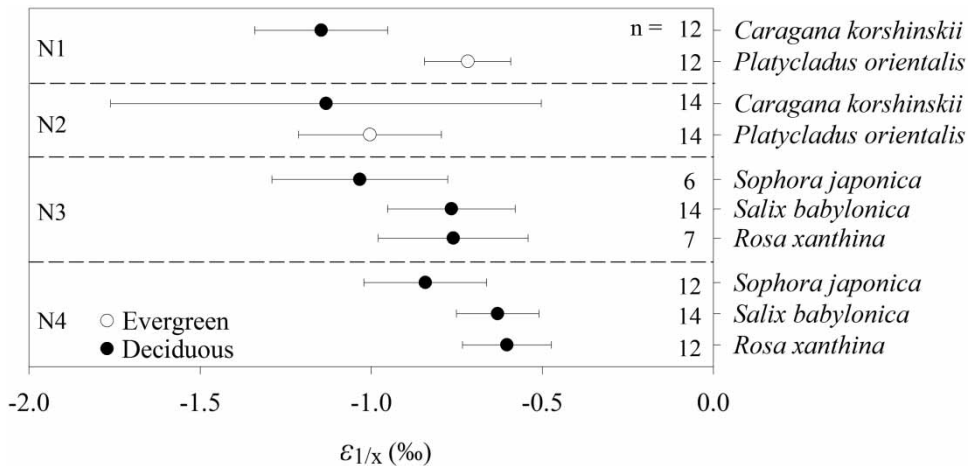


Figure 4 | Seasonal variations of  $\delta D_{LMWL-int}$  and ED value of xylem water from four sampling sites ( $n$ : number of samples; N1, N2, N3, and N4 denote the four sampling sites).





**Figure 5** | The enrichment factor ( $\epsilon_{1/x}$ ) of xylem-to-leaf water among different species, leaf phenology, and sampling sites.

showed that the average  $\epsilon_{1/x}$  was  $-0.91 \pm 0.36\text{‰}$  at all sampling sites and for all plant species (trees and shrubs only). The  $\epsilon_{1/x}$  exhibited significant differences between four sites plants, with mean values:  $-0.89 \pm 0.16\text{‰}$  at N1,  $-1.07 \pm 0.46\text{‰}$  at N2,  $-0.76 \pm 0.19\text{‰}$  at N3, and  $-0.62 \pm 0.12\text{‰}$  at N4. The  $\epsilon_{1/x}$  values were classified as follows:  $N4 > N3 > N1 > N2$ , indicating that the evaporation of leaf water decreased with elevation. Kahmen et al. (2013) noted that the enrichment of  $\delta D$  was stronger in arid biomes (40–100‰), intermediate in temperate biomes (10–30‰), and weaker in humid tropical biomes (0–20‰). Some studies have also shown that air temperature, relative humidity, wind speed, and  $\delta D$  of atmospheric water vapor influences the leaf water deuterium enrichment (Sachse et al. 2004). In our study, the broad range of measured  $\delta D_{\text{leaf}}$  values (ranging from  $-44.25\text{‰}$  to  $59.35\text{‰}$ ) was not surprising because several environmental variables, the monthly average air temperature, and the precipitation amount varied significantly (Figure 2) and affected greatly the variability of  $\delta D_{\text{leaf}}$  and  $\epsilon_{1/x}$  between different months.

## DISCUSSION

### Different isotopic signatures of precipitation, river water, and soil water

In arid and semi-arid regions, precipitation is the primary source of water for plants. Water use competition between

plants is more significant during the dry season, and in order to avoid fierce competition for water, plants have developed different water-use strategies to cope with water shortages or water stress. In our study area, over 76% of precipitation occurred in the 2016 summer, and the  $\delta D_{\text{prec}}$  and  $\delta^{18}\text{O}_{\text{prec}}$  values exhibited the rainfall-amount effect (Dansgaard 1964). The mean  $\delta^{18}\text{O}_{\text{prec}}$  value showed significant seasonal fluctuations, with enriched values occurring in summer and autumn, and depleted values in spring. However, xylem water (both trees and shrubs) isotopic compositions across all sites were significantly depleted compared to the precipitation values in spring (Table 2). Soil water also experienced significant enrichment during this season.

Soil water is the immediate water source for plants. The isotopic compositions of soil water at four sampling sites showed a clear isotopic depletion with depth (Table 2). The shallow soil water at sites N1, N2, and N3 isotopically enriched in the wet season and depleted in the dry season, which was synchronized with the seasonal variations of the isotopic composition in precipitation. This pattern was the result of both precipitation pulse inputs and evaporation enrichment. The isotopic compositions of middle soil water presented a depletion in the wet season and an enrichment in the dry season at sites N1, N2, and N3. The deep soil water isotopically depleted in the wet season and enriched in the dry season at sites N1 and N3, while site N2 was the opposite. At site N4, the isotopic value was gradually depleted with soil depth, but the layers were close to the

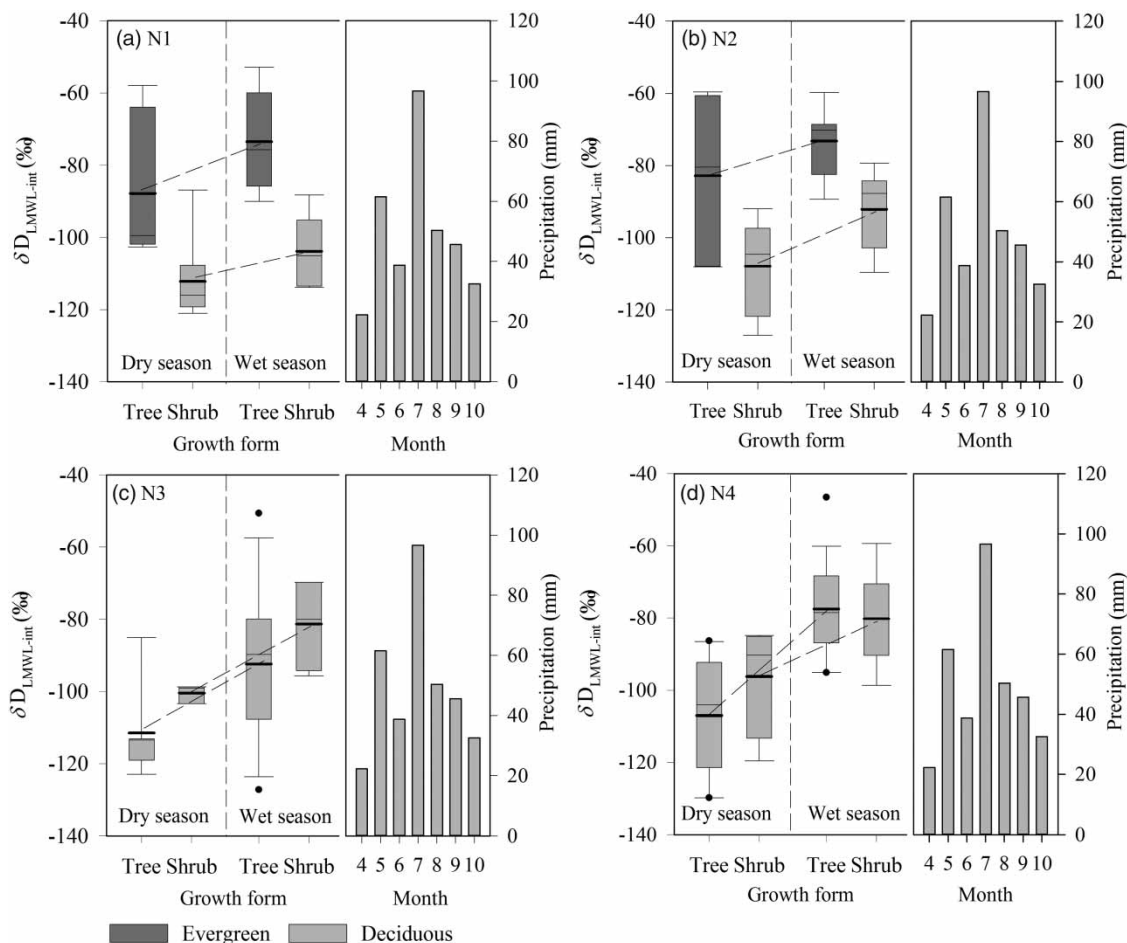
isotopic values of the river water in both the dry and wet seasons.

### Spatial and seasonal partitioning of plant water sources

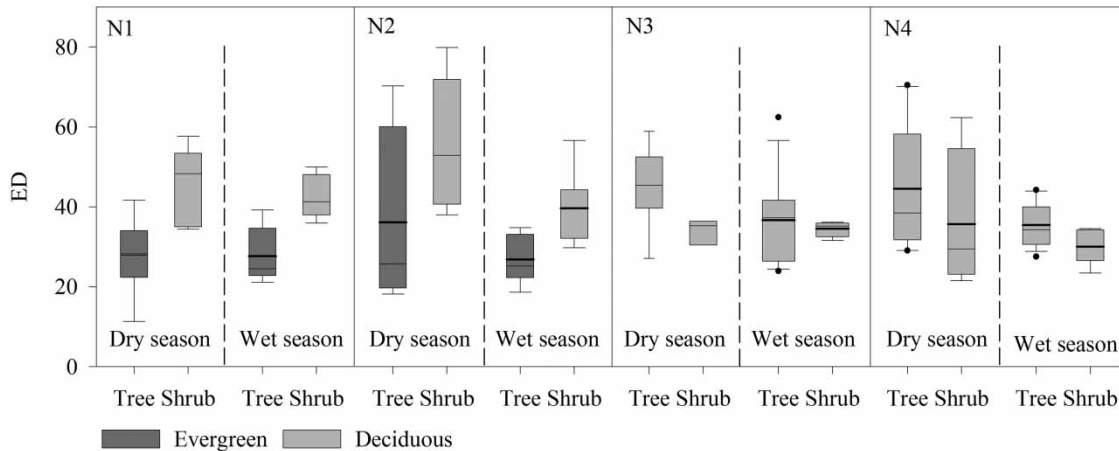
The average isotopic composition of the source of xylem water was reflected in the intersection points of individual xylem sample LEL with the LMWL. Plants that relied mostly on water from isotopically enriched precipitation during the wet season would exhibit relatively high  $\delta D_{LMWL-int}$  values (Figure 6), while the opposite was true for plants that relied on isotopically depleted precipitation in the dry season. The ED value was proportional to the relative degree of evaporation before uptake by the plants. The higher this ED, the greater the relative importance of

shallow soil water (which was prone to evaporation) compared to deeper soil water. In our study area, Chen *et al.* (2015) found that the  $\delta^{18}O$  and  $\delta D$  values of precipitation enriched from May to September and depleted from October to April of the next year. As shown in Table 2, at the sites N1, N2, and N3, shallow soil water isotopically depleted in the dry season and enriched in the wet season, which was similar to the variations of precipitation isotopic compositions.

Whether in the dry or wet season, the leaf phenology of plant had significant impact on  $\delta D_{LMWL-int}$  and ED at sites N1 and N2 (Figure 6 and 7), where the ED value of evergreen plants was lower than that of the deciduous, suggesting that evergreen plants would have been adapted to water tapping from deep soil water sources (e.g. isotopic



**Figure 6** | Seasonal variations of precipitation amount and  $\delta D_{LMWL-int}$  value among different sampling sites, growth form, and leaf phenology of plants.



**Figure 7** | The ED values of plants as a function of the sampling sites, growth form, and leaf phenology.

depleted water), which allows them to survive the long dry season, as observed by Jackson *et al.* (1995) in a tropical moist lowland forest in Panama.

At sites N1 and N2, the mean ED value of trees was lower than that of shrubs during the dry season or wet season (Figure 7), indicating that trees used more deep soil water. In contrast, at site N3, the mean ED value of trees was higher than that of shrubs, indicating that trees used more shallow soil water enriched in heavy isotopes by evaporation. It was generally accepted that the deeper root systems of trees compared to shrubs allowed them to access deeper soil water or groundwater (Evaristo & McDonnell 2017). However, Meinzer *et al.* (1999) found that smaller trees used deeper sources of water than larger trees, and attributed this to three possible factors. In our study, the ED values of plants (both trees and shrubs) at site N4 were strikingly higher than that of plants growing at sites N1 and N2 (Figure 7). This was because plants in this site used more river water, which had relatively depleted  $\delta D_{\text{river}}$  and  $\delta^{18}O_{\text{river}}$ . In general, the ED value of trees and shrubs were closer in the wet season because there was more precipitation for plants to uptake. During the dry season, the differences of ED values between trees and shrubs were relatively large, indicating differences in water source depths. This suggests that water competition among different plant species was mitigated during the dry season due to water resource partitioning.

Plants in all four sites showed similar, very high  $\delta D_{\text{LMWL-int}}$  values from June to September, indicating that

plants relied mostly on enriched precipitation during this period. The  $\delta D_{\text{LMWL-int}}$  value of plants sampled in October was close to the  $\delta D_{\text{LMWL-int}}$  in September because the precipitation represented the onset of the short wet season following a dry season and the soil was expected to recharge. This is following the ‘two water world’ hypothesis of Brooks *et al.* (2010). From observations it was obvious that site N4 was the wettest of all four local sites, and plants remained green in the dry season because there was plenty of river water available. Plants at sites N1, N2, and N3 showed lowest  $\delta D_{\text{LMWL-int}}$  values in April, which then increased during the following months to reach their peak values in September. This indicates that the water pool for the plants was replenished stepwise by the isotopically more enriched precipitation. At site N1 and N2, plants showed strong seasonal trends in  $\delta D_{\text{LMWL-int}}$ , and the seasonal trends were more pronounced than at site N3. This is probably because site N3 was affected by irrigation water coming from the Yellow River. We did not measure the isotopic composition of irrigation water at site N3, but in this study the isotopic value of irrigation water is close to river water.

From all plants at four sampling sites, trees and shrubs exhibited different water-use patterns that might be related to the distribution of their roots and to the physiological characteristics of the same habitat (Ward *et al.* 2013). For example, the surface roots of *Platyclusus orientalis* are more developed—about 50% of their root biomass is located in the surface layer (Evaristo & McDonnell 2017). The surface roots developed by *P. orientalis* are sensitive to

precipitation responses and can be used to absorb surface water with higher water content through their developed root tip after a rain event (Liu et al. 2016). In addition to the effect of the roots on the water-use patterns of plants, the plants themselves affect the soil. The threshold value of response of SWC also affects the water use of plants (Han et al. 2009).

### Parameters influencing xylem-to-leaf deuterium enrichment

Leaf phenology significantly influenced the  $\varepsilon_{l/x}$ . The  $\varepsilon_{l/x}$  values of evergreen plants were generally higher than those of the deciduous plants at sites N1 and N2 (Figure 5). Evergreen plants that keep their foliage during the dry season must be protected against drought stress by a high degree of succulence or sclerophylly (thickened or hardened leaves) in order to reduce moisture loss (Chabot & Hicks 1982). Thus, the adaptive traits of the evergreens that reduce water loss and transpiration rates causes a lower xylem-to-leaf deuterium enrichment. The differences in  $\varepsilon_{l/x}$  between the four sampling sites were obvious: the  $\varepsilon_{l/x}$  values were lower at sites N1 and N2 but higher at sites

N3 and N4, indicating that the location (elevation) of the plants significantly affected the  $\varepsilon_{l/x}$ . For example, the  $\varepsilon_{l/x}$  values of *Caragana korshinskii* (sites N1 and N2), *Sophora japonica*, and *Rosa xanthina* (sites N3 and N4) varied significantly between the different sites. However, the  $\varepsilon_{l/x}$  values of *Salix babylonica* and *P. orientalis* changed slightly, irrespective of their sampling sites. We can see that the overall difference between  $\varepsilon_{l/x}$  values among the different sampling sites was due to differences between plant assemblage or features at each site rather than to habitat-specific (environment conditions) factors. Growth forms did not significantly affect the  $\varepsilon_{l/x}$  in the study area. For example, the mean  $\varepsilon_{l/x}$  values of trees and shrubs were  $-0.84 \pm 0.22\text{‰}$  and  $-1.03 \pm 0.50\text{‰}$ , respectively. The variations of season also influenced the  $\varepsilon_{l/x}$  value of the plant species (Figure 8): during April and June all species were characterized by lower  $\varepsilon_{l/x}$  values, but were higher during May and July. In August, September, and October, the difference between the  $\varepsilon_{l/x}$  values were not significant. The  $\varepsilon_{l/x}$  value reached its peak in July with higher temperatures and more precipitation, but in June with higher temperatures, the  $\varepsilon_{l/x}$  value reached a minimum. There was no obvious correlation between the  $\varepsilon_{l/x}$  value and temperature or precipitation.

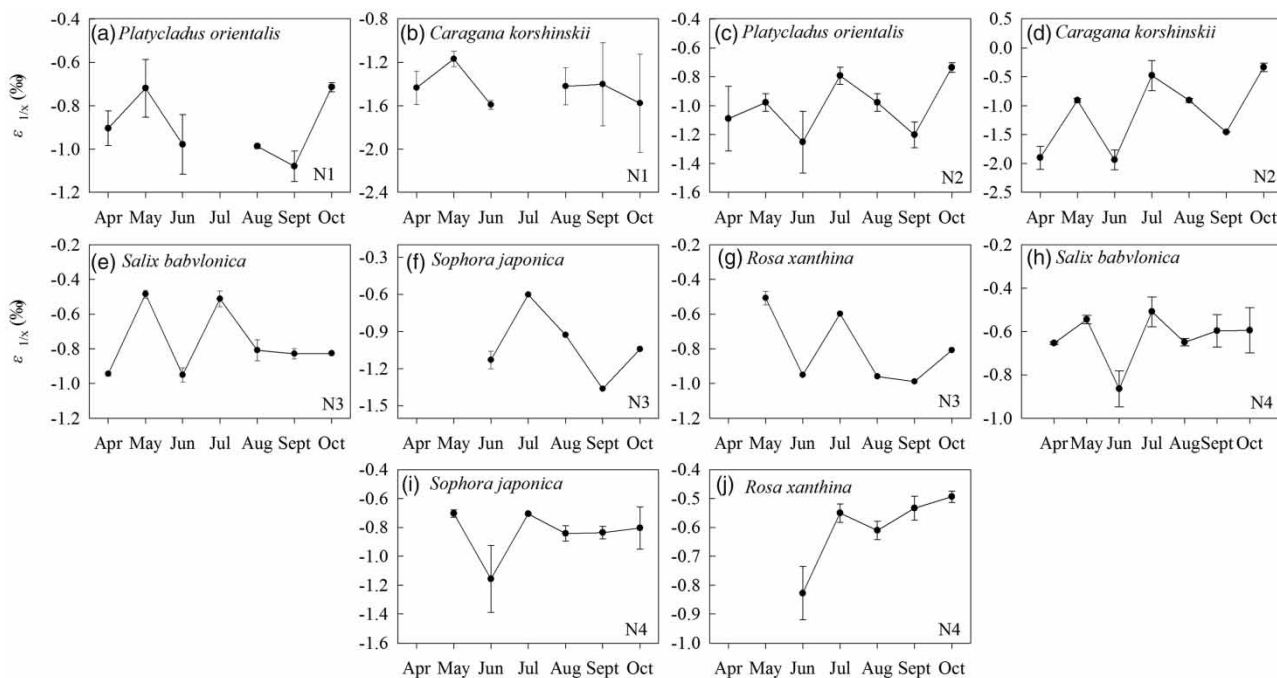


Figure 8 | Temporal variations of  $\varepsilon_{l/x}$  value across different plant species.

In summary, our results showed that on the local scale of a single study area, with several distinct plant sampling sites, the plant species assemblage and leaf phenology were the primary factors influencing xylem-to-leaf water deuterium enrichment. Seasonality also influences the  $\epsilon_{1/x}$  values, while local elevation and growth form had negligible effects.

## CONCLUSIONS

In this study, we measured the  $\delta D$  and  $\delta^{18}O$  of precipitation, river water, soil water, and plant xylem and leaf water during the 2016 growth season at four sampling sites in Lanzhou. The conclusions are summarized as follows:

- (1) Plant water resource partitioning during the 2016 growing season varied both in time and space, as inferred by the relationship between the  $\delta D_{\text{xylem}}$  values and the different water sources and ED values. During the wet season, plants exhibiting relatively high  $\delta D_{\text{LMWL-int}}$  values relied mostly on water from isotopically enriched precipitation. During the dry season, the differences of ED values between trees and shrubs were relatively large, indicating differences in water source depths. The leaf phenology of the plant had a significant impact on  $\delta D_{\text{LMWL-int}}$  and ED values, whereas growth form did not significantly influence the values.
- (2) The mean value of xylem-to-leaf water deuterium enrichment ( $\epsilon_{1/x}$ ) was  $-0.91 \pm 0.36\text{‰}$  for all plant species, seasons, and sampling sites. Plant species, leaf phenology, and seasons were the primary factors influencing the  $\epsilon_{1/x}$ , while growth form and elevation had negligible effects. In terms of plants leaf phenology, the deciduous species gave the highest enrichment. In terms of different seasons, plants showed the highest isotopic enrichment in July.

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## REFERENCES

- Allen, S. T., Kirchner, J. W., Braun, S., Siegwolf, R. T. W. & Goldsmith, G. R. 2019 *Seasonal origins of soil water used by trees*. *Hydrology and Earth System Sciences* **23**, 1199–1210. <https://doi.org/10.5194/hess-23-1199-2019>.
- Asbjornsen, H., Mora, G. & Helmers, M. J. 2007 *Variation in water uptake dynamics among contrasting agricultural and native plant communities in the Midwestern US*. *Agriculture Ecosystems Environment* **121** (4), 343–356. <https://doi.org/10.1016/j.agee.2006.11.009>.
- Barbeta, A. & Peñuelas, J. 2017 *Relative contribution of groundwater to plant transpiration estimated with stable isotopes*. *Scientific Reports* **7** (1), 10580. <https://doi.org/10.1038/s41598-017-09643-x>.
- Barbour, M. M., Farquhar, G. D. & Buckley, T. N. 2017 *Leaf water stable isotopes and water transport outside the xylem*. *Plant Cell & Environment* **40** (6), 914–920. <https://doi.org/10.1111/pce.12845>.
- Brooks, J., Barnard, H., Coulombe, R. & McDonnell, J. 2010 *Ecohydrologic separation of water between trees and streams in a Mediterranean climate*. *Nature Geoscience* **3** (2), 100–104. [https://doi.org/10.1038/NEG\\_0722](https://doi.org/10.1038/NEG_0722).
- Chabot, B. F. & Hicks, D. J. 1982 *The ecology of leaf life spans*. *Annual Review of Ecology and Systematics* **13** (1), 229–259. <https://doi.org/10.1146/annurev.es.13.110182.001305>.
- Chen, F. L., Zhang, M. J., Ma, Q., Wang, S. J., Li, X. F. & Zhu, X. F. 2015 *Stable isotopic characteristics of precipitation in Lanzhou City and its surrounding areas*. *Northwest China Environment Earth Sciences* **73** (8), 4671–4680. <https://doi.org/10.1007/s12665-014-3776-6>.
- Chen, H., Wang, B., Xia, D. S., Fan, Y. J., Liu, H., Tang, Z. R. & Ma, S. 2019 *Magnetic characteristics of Juniperus formosana needles along an urban street in Lanzhou, Northwest China: the variation of different season and orientation*. *Environmental Science and Pollution Research* **26** (21), 21964–21971. <https://doi.org/10.1007/s11356-019-05399-1>.
- Coenders-Gerrits, A. M. J., Van der Ent, R. J., Bogaard, T. A., Wang-Erlandsson, L., Hrachowitz, M. & Savenije, H. H. G. 2014 *Uncertainties in transpiration estimates*. *Nature* **506** (7487), E1–E2. <https://doi.org/10.1038/nature12925>.
- Dansgaard, W. 1964 *Stable isotope in precipitation*. *Tellus* **16**, 436–468. <https://doi.org/10.3402/tellusa.v16i4.8993>.
- Dawson, T. E. & Ehleringer, J. R. 1991 *Streamside trees that do not use stream water*. *Nature* **350**, 335–337. <https://doi.org/10.1038/350335a0>.
- Evaristo, J. & McDonnell, J. J. 2017 *Prevalence and magnitude of groundwater use by vegetation: a global stable isotope meta-analysis*. *Scientific Reports* **7**, 44110. <https://doi.org/10.1038/srep44110>.
- Filella, I. & Peñuelas, J. 2003 *Partitioning of water and nitrogen in co-occurring Mediterranean woody shrub species of different evolutionary history*. *Oecologia* **137**, 51–61. <https://doi.org/10.1007/s00442-003-1333-1>.

- Goldsmith, G. R., Muñoz-Villers, L. E., Holwerda, F., McDonnell, J. J., Asbjornsen, H. & Dawson, T. E. 2011 [Stable isotopes reveal linkages among ecohydrological processes in a seasonally dry tropical montane cloud forest](#). *Ecohydrology* **5** (6), 779–790. <https://doi.org/10.1002/eco.268>.
- Goldsmith, G. R., Allen, S. T., Braun, S., Engbersen, N., Romero González-Quijano, C., Kirchner, J. W. & Siegwolf, R. T. W. 2018 [Spatial variation in throughfall, soil, and plant water isotopes in a temperate forest](#). *Ecohydrology* e2059. <https://doi.org/10.1002/eco.2059>.
- Han, L. B., Wang, Q., Wang, X. P., Gu, Z. Y., Du, Y. J. & Song, G. L. 2009 [Researches on root distribution of \*Vitex negundo\* var. \*Heterophylla\* \(Franch.\) Rehd. on different sites conditions](#). *Journal of Basic Science and Engineering* **17**, 231–237. (in Chinese).
- Hervé-Fernández, P., Oyarzún, C., Brumbt, C., Huygens, D., Bodé, S., Verhoest, N. E. C. & Boeckx, P. 2016 [Assessing the 'two water worlds' hypothesis and water sources for native and exotic evergreen species in south-central Chile](#). *Hydrological Processes* **30** (23), 4227–4241. <https://doi.org/10.1002/hyp.10984>.
- Holloway-Phillips, M., Cernusak, L. A., Barbour, M., Song, X., Cheesman, A., Munksgaard, N., Stuart-Williams, H. & Farquhar, G. D. 2016 [Leaf vein fraction influences the Péclét effect and  \$^{18}\text{O}\$  enrichment in leaf water](#). *Plant, Cell & Environment* **39** (11), 2414–2427. <https://doi.org/10.1111/pce.12792>.
- Jackson, P. C., Cavelier, J., Goldstein, G., Meinzer, F. C. & Holbrook, N. M. 1995 [Partitioning of water resources among plants of a lowland tropical forest](#). *Oecologia* **101** (2), 197–203. <https://doi.org/10.1007/BF00317284>.
- Kahmen, A., Hoffmann, B., Schefuss, E., Arndt, S. K., Cernusak, L. A., West, J. B. & Sachse, D. 2013 [Leaf water deuterium enrichment shapes leaf wax n-alkane  \$\delta\text{D}\$  values of angiosperm plants II: observational evidence and global implications](#). *Geochimica et Cosmochim. Acta* **111**, 50–63. <https://doi.org/10.1016/j.gca.2012.09.004>.
- Kahmen, A., Sachse, D., Arndt, S. K., Tu, K. P., Farrington, H., Vitousek, P. M. & Dawson, T. E. 2011 [Cellulose  \$\delta^{18}\text{O}\$  is an index of leaf-to-air vapor pressure difference in tropical plants](#). *Proceedings of the National Academy of Sciences* **108** (5), 1981–1986. <https://doi.org/10.1073/pnas.1018906108>.
- Lin, G. H. & Sternber, L. S. L. 1993 [Hydrogen isotopic fractionation by plant roots during water uptake in coastal wetland plants](#). In: *Stable Isotopes and Plant Carbon/Water Relations*. Academic Press, New York, pp. 497–510. <https://doi.org/10.1016/B978-0-08-091801-3.50041-6>.
- Liu, Z. Q., Yu, X. X., Deng, W. P., Jia, G. D., Jia, J. B., Lou, Y. H. & Li, H. Z. 2016 [Water sources of \*Pinus tabulaeformis\* and \*Platycladus orientalis\* before and after rain in northern China](#). *Science of Soil and Water Conservation* **14**, 112–119 (in Chinese).
- Meinzer, F. C., Andrade, J. L., Goldstein, G., Holbrook, M. N., Cavelier, J. & Wright, S. J. 1999 [Partitioning of soil water among canopy trees in a seasonally dry tropical forest](#). *Oecologia* **121** (3), 293–301. <https://doi.org/10.1007/s004420050931>.
- Palacio, S., Montserrat-Martí, G. & Ferrio, J. P. 2017 [Water use segregation among plants with contrasting root depth and distribution along gypsum hills](#). *Journal of Vegetation Science* **28** (6), 1107–1117. <https://doi.org/10.1111/jvs.12570>.
- Rozanski, K., Araguás-Araguás, L. & Gonfiantini, R. 1993 [Isotopic patterns in modern global precipitation](#). *Geophysical Monograph* **78**, 1–35. <https://doi.org/10.1029/GM078p0001>.
- Sachse, D., Radke, J. & Gleixner, G. 2004 [Hydrogen isotope ratios of recent lacustrine sedimentary n-alkane record modern climate variability](#). *Geochimica et Cosmochimica Acta* **63** (23), 4877–4889. <https://doi.org/10.1016/j.gca.2004.06.004>.
- Schenk, H. J. & Jackson, R. B. 2002 [Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems](#). *Journal of Ecology* **90** (3), 480–494. <https://doi.org/10.1046/j.1365-2745.2002.00682.x>.
- Schnitzer, S. A. & Bongers, F. 2011 [Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms](#). *Ecology Letters* **14** (4), 397–406. <https://doi.org/10.1111/j.1461-0248.2011.01590.x>.
- Sohel, M. S., Salam, M. A. & Herbohn, J. 2019 [An assessment of woody plant water source studies from across the globe: what do we know after 30 years of research and where do we go from here?](#) *Hydrology* **6**, 40. <https://doi.org/10.3390/hydrology6020040>.
- Sprenger, M., Llorens, P., Cayuela, C., Gallart, F. & Latron, J. 2019 [Mechanisms of consistently disjunct soil water pools over \(pore\) space and time](#). *Hydrology and Earth System Sciences* **23**, 2751–2762. <https://doi.org/10.5194/hess-23-2751-2019>.
- Stratton, L. C., Goldstein, G. & Meinzer, F. C. 2000 [Temporal and spatial partitioning of water resources among eight woody species in a Hawaiian dry forest](#). *Oecologia* **124** (3), 309–317. <https://doi.org/10.1007/s004420000384>.
- Wang, J., Lu, N. & Fu, B. 2019 [Inter-comparison of stable isotope mixing models for determining plant water source partitioning](#). *Science of the Total Environment* **666**, 685–693. <https://doi.org/10.1016/j.scitotenv.2019.02.262>.
- Ward, D., Wiegand, K. & Getzin, S. 2013 [Walter's two-layer hypothesis revisited: back to the roots!](#) *Oecologia* **172** (3), 617–630. <https://doi.org/10.1007/s00442-012-2538-y>.
- Wu, H., Li, X. Y., Jiang, Z., Chen, H., Zhang, C. & Xiao, X. 2016 [Contrasting water use pattern of introduced and native plants in an alpine desert ecosystem, Northeast Qinghai-Tibet Plateau, China](#). *Science of the Total Environment* **542**, 182–191. <https://doi.org/10.1016/j.scitotenv.2015.10.121>.
- Yaseef, N. R., Yakir, D., Rotenberg, E., Schiller, G. & Cohen, S. 2010 [Ecohydrology of a semi-arid forest: partitioning among water balance components and its implications for predicted precipitation changes](#). *Ecohydrology* **3** (2), 143–154. <https://doi.org/10.1002/eco.65>.