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A novel approach for estimating groundwater use by plants in rockdominated habitats

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ABSTRACT

Plant water use is an important component in the function of Earth's critical zone and this can be examined by decomposing isotope composition of xylem water into contributions from precipitation stored in shallow soil layers and deeper groundwater. The usual procedure for estimating the proportional use of groundwater by plants is to sample the isotope composition of soil and groundwater and determine the most probable mixing coefficients from all potential sources. Here we propose and test a novel method for achieving the same goal without sampling soil water. The method is based on analyzing variability in the stem water isotope ratios of several members of a community and the known isotope ratio of groundwater to 'triangulate' the unknown isotope ratio of stored rainwater. Using a simple water balance model, parameterized to produce the best fit between actual and estimated stem water isotope ratios, we simulated seasonal variation in the volume and isotope ratio of rainwater storage, along with species-specific groundwater use ratios. The method was applied to eight woody plant species growing on two rocky outcrops in the South China karst. Estimated average proportional groundwater use over two seasons varied between 14% and 62% and was site-dependent. For the majority of species, groundwater use increased as estimated stored rainwater volume declined. The two species with highest groundwater use were taller, deciduous or semi-deciduous trees with lower wood densities. While the new method was inspired by the inability to sample water stored in the rocky outcrops, it may have broader use in any environment where the spatial variability of soil water isotope composition is a barrier to estimating average groundwater use ratios. The broader adoption of this or equivalent methods would greatly improve the study of the Earth's critical zone.

1. Introduction

The fate of precipitation at the terrestrial surface is a central issue in the study of Earth's critical zone (Fan, 2015; Grant and Dietrich, 2017). At this interface of ground and atmosphere, precipitation is divided between the proportion that is returned to the atmosphere, feeding back on climate systems, and the proportion that becomes streamflow and groundwater, providing water for humans and aquatic ecosystems (Good et al., 2015; Schlesinger and Jasechko, 2014). Climate and the biological and physical structure of the interface control the partitioning of precipitation, but there is debate over how much control is exerted by each factor (Evaristo et al., 2015; Kim and Jackson, 2012).

The hydrological balance of woodlands is largely determined by woody plant transpiration, which in turn depends on atmospheric conditions (potential evapotranspiration; PET), water availability near the surface and potentially complex interactions with shallow groundwater reservoirs ranging from inhibiting water uptake due to root inundation to subsidizing the local water budget (Allen et al., 2016; Zolfaghar et al., 2017). The interactions between wooded ecosystems and groundwater are of potentially far-reaching consequences for ecosystem health and society, as increases in groundwater extraction for agriculture may endanger groundwater-dependent ecosystems in some

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Fig. 1. The location of experimental area (a) and the location of the springs and the experimental outcrop in the catchment (b), the cross section of the topographic structures (c).

regions (Eamus et al., 2015), whereas deforestation in other regions may increase flood potential and intensity (Bradshaw et al., 2007).

Many studies have been conducted across a wide range of ecosystems to determine how much groundwater is taken up by woody plants (Evaristo and McDonnell, 2017; Rossatto et al., 2012; Steggles et al., 2017; Zencich et al., 2002). One of the established methods for estimating groundwater use is the stable isotope analysis of plant xylem water. Excluding some halophytic and xerophytic plants (Ellsworth and Williams, 2007), plants do not fractionate hydrogen and oxygen isotopes during water uptake, so that xylem water can be assumed to be a volume-weighted mixture of all plant water sources including surficial water and, potentially, deeper groundwater (Lin et al., 1993). If the isotope ratios of all potential plant water sources are known, and they are sufficiently distinct in both δD and $\delta^{18}O$ values, the proportional contributions from up to three water sources can be inferred (Asbjornsen et al., 2007; Ehleringer and Dawson, 1992; Ogle and Reynolds, 2004).

Three important challenges exist for the success of isotopic tracing method: First, representative samples of all water sources must be obtainable; second, predetermined pools of water that the study seeks to distinguish (e.g. soil water versus groundwater) must be isotopically distinct, and third, samples should be taken repeatedly to be representative of natural fluctuation in available water. (Brunel et al., 1995; Dawson et al., 2002). The first challenge can be constraining in

landscapes with scarce soil cover, such as on the rocky slopes of uplands or in karst regions where roots draw water from rock fractures (Hubbert et al., 2001; Nie et al., 2012; Querejeta et al., 2006; Rong et al., 2011). The problem here is that, without a major excavation effort, it is virtually impossible to sample water stored in rock fractures. But even if there is soil to sample, isotopic variation can be high, typically producing a wide margin of error in the estimation of water source contribution. The second challenge is not an obstacle in most climate zones where evaporative enrichment of surface water creates a pool of water uniquely different from deeper water sources or groundwater (Ehleringer et al., 1991). But it may be an obstacle in the tropics, where high humidity, frequent rain and a low contribution of evaporation in evapotranspiration may limit evaporative enrichment of the soil (Gibson et al., 2008), although recent studies in two tropical watersheds determined that soil water and groundwater can still be distinguished in dual-isotope space (Evaristo et al., 2016).

The third challenge is that the frequent sampling that would be required to estimate seasonally-integrated water use is costly and time consuming and therefore rarely done. The vast majority of studies capture a limited number of snapshots through time, typically focused the hydrologically extremes of the peak rainy season and the end of the dry season (Evaristo and McDonnell, 2017). This is instructive in terms of bracketing the extremes of plant water use, for example, highlighting species differences in accessing deeper water sources during drought (Dawson and Pate, 1996) or in their ability to switch to shallow water sources after rain (West et al., 2007). But such limited sampling is insufficient to estimate seasonally integrated patterns of plant water use.

Here, we introduce a novel method for collecting and analyzing plant water isotope samples that overcomes all three limitations, i.e., source inaccessibility, inconsistent isotopic distinction and limited sample size. In a nutshell, the method is based on analyzing the joint variation in the stem water isotope ratios of individual plants over time and assuming that the driver of this variation is the near-surface water source used by all plants, albeit in variable proportions. Thus, we operationalize 'shallow water' as a dynamic water pool that frequently shifts hydrogen and oxygen isotope ratios by evaporative enrichment and mixing stored water with new precipitation inputs, and is well mixed, if not at the source, then during uptake through extensive and intermingled plant root systems. To constrain the analysis, we also sample precipitation, in addition to groundwater as a second feasible plant water source and estimate the evaporative enrichment of stored water based on a simplified version of the Craig-Gordon model (Craig and Gordon, 1965). This procedure amounts to substantial time savings, not only in terms of obtaining soil samples but also in eliminating the need for water extraction. Finally, by assuming simple soil behaviors, sampling efforts can focus on characterizing stem samples more often and for longer periods of time, so that seasonal and annual averages of shallow vs groundwater use can be obtained.

We tested this idea in the South China karst. Typical of karst regions worldwide, soils in this region are thin and plant roots grow into the 'epikarst', the highly weathered 'skin of the karst' (Bakalowicz, 2004) growing along cracks and crevices (Bonacci et al., 2009; Stothoff et al., 1999). Given the structural heterogeneity intrinsic to this landform, it is patently impossible to classify plant water sources by depth layers, as done in ecosystems where precipitation infiltrates from the top of the soil downwards (Barnes and Allison, 1988). In epikarst, storage pools for water are composed of a collection of cracks and fissures through which water percolates at variable speeds, and solution-enhanced cavities that collect water at the interface with impervious rock (Fig. 1c). Pockets of slow-moving or stagnant water are readily refilled by precipitation and depleted by evapotranspiration. This pool is largely disconnected from the conduits that fill water tables that may be perched at the bottom of the epikarst and can issue from springs at the bottom of hill slopes (Guo et al., 2015; Jones, 2010; Schwartz et al., 2013). This water pool is replenished through deep fissures, including at higher elevation, and by slow drip from diffuse discharge points throughout the epikarst. The higher residence time of water in the perched water table stabilizes isotope ratios, which for this ecosystem is close to the volume-weighted isotope ratio of annual precipitation. However, high-volume precipitation events can temporarily move the isotope ratio of spring water a few permille away from the baseflow average.

Based on this model, we distinguish two water sources for plants growing on epikarst outcrops, one that is highly accessible to woody plant roots, frequently recharged by precipitation and subject to evaporative enrichment ('shallow'), and another pool that is comparatively static due to slow or infrequent recharge and lack of evaporative enrichment (groundwater).

Using a water budget model, we simulate the dynamics of the shallow water pool using precipitation volume and isotope ratios as input and estimating the water loss rate and evaporative enrichment by maximizing the fit between estimated and measured isotope ratios in plants. We applied the technique to eight woody plant species located across two rocky outcrops in one watershed of the South China karst. The goal of the study was to ascertain whether and to what extent the species differed in groundwater use, and whether the method for estimating groundwater use produce consistent results across two independently parameterized rocky outcrops. Additionally, in the second year of the study, we sought to determine plant response to water limitations, by covering one of the outcrops with a transparent plastic sheet, thereby preventing its recharge for a month in the late growing season.

2. Materials and methods

2.1. Site description and rainfall manipulation

The experimental sites were situated at Huanjiang Observation and Research Station for Karst Ecosystems administrated by the Chinese Academy of Sciences, a typical karstic peak-cluster depression with an area of 146.1 ha, which is located in Guangxi Province, southwest (24°43′58.9″–24°44′48.8″N. 108°18′56.9″–108°19′58.4″E) China (Fig. 1a and b). Climate in the research station is subtropical mountainous monsoon climate, with mean annual precipitation of 1390 mm and average annual air temperature of 18.5 °C. Rainfall mostly occurs at the end of April to early September (Chen et al., 2011). About 60% of the hillslopes in this catchment are dominated by shallow soil (10-30 cm on average) and loose rocky habitats. Expansion of these habitats is frequently interrupted by the appearance of isolated rocky outcrops, which characterized by thin and little soil on the surface and litter filled cracks, fissures, and channels internally. Because of the harshness of the environment, the most common vegetation are tussock and scrubland. Big trees are usually found on the deep soils at the foot of hillslopes, or on rocky outcrops and nearby soils (Nie et al., 2011).

The study focused on two large, isolated dolomite outcrops covered by dense vegetation and dominated by species adapted to rocky habitat. Plants usually emerge from cracks directly or grow on protuberant rocks with roots grown into cracks. Outcrop 1 is cube-shaped with a rough surface of about 8 m in length and 12.5 m in width, Outcrop 2 was 10 m in length and 15 m in width. Both rose approximately 8 m high above the hillslope. To create differences in rainfall input in the second year of the study, Outcrop 2 was covered with a clear plastic sheet from August 2–18, withholding the approximately 57 mm of rain that fell over this period. The experiment was intended to last longer but was cut short by strong winds, which damaged the cover and the cover was subsequently removed.

2.2. Sample collection

The water of individual rain events was collected for nearly two years between January 2014 and September 2015, following the protocol of the Global Network of Isotopes in Precipitation (IAEA and WMO, 2006). When it rained, precipitation samples were collected once or twice a day. Rainfall quantity was measured at a meteorological station located in the same small watershed. We also obtained data to calculate daily *PET* values using the Penman-Monteith equation (Allen et al., 1998) from this station.

Groundwater was collected from a spring almost every two weeks in 2014 from two springs at the experimental station. One of the springs was located at the foot of the hill directly below the outcrop 1 and 2. Isotope values did not differ much between collection points and over time, so we omitted collecting groundwater in 2015. Diameter at breast height (DBH) and height of each plant was measured with rods and tapes. We calculated specific leaf area (SLA) as the ratio of leaf area to dry mass. About 30-50 fresh clean leaves from the broadleaved species were randomly selected from each plastic zip-lock bag and measured by CI-203 (CID Inc, USA) to determine leaf area. These leaves were subsequently oven dried at 75 °C to constant weight. The total mass of all the dried leaves was measured and divided by the total leaf number to determine the average leaf dry mass for each sampling time. Dry mass of the leaves was measured by an electron balance (Mettler-Toledo, China, e = 1 mg, d = 0.1 mg). Wood density values of bark removed stem were oven dry mass per saturated volume (g/cm³). The volume was measured by a graduated cylinder.

Eight woody plant species (six on Outcrop 1, five on Outcrop 2) were selected for the study (Table A1). They comprised deciduous and

semi-deciduous tree species as well as one evergreen shrub in the understory.

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Stem samples for isotope analysis were taken monthly from April to November in the first year of the study (2014: April 18, May 25, June 29, July 31, August 31, September 26, October 28, and November 30) and from March to September in the second year (2015: March 31, May 7, June 7, August 1, 4, 11, 22, and September 27). The second year contained an interval of higher frequency sampling during the period that Outcrop 1 was covered. Samples were taken on three individuals per species and outcrop. Stem samples were taken well below the leafed portion of the stem to reduce the risk of back-diffusion of evaporatively enriched leaf water (Schwinning, 2008). In addition, bark was removed to avoid possible contamination of xylem water by isotopically enriched water in the cortex (Brunel et al., 1995; Ehleringer and Dawson, 1992). Samples were immediately placed in a capped vial, wrapped in parafilm, and placed in a cooler with ice for transportation to the laboratory. Then they were frozen until further processing.

2.3. Water extraction and isotope analysis

Water was extracted from plant stem samples using cryogenic vacuum distillation (Ehleringer et al., 2000). The deuterium and oxygen ratios of precipitation and stem water were measured with a liquid water isotope laser spectroscopy instrument (Model DLT-100, LGR Inc.) at the Key Laboratory of Agro-Ecological Processes in the Institute of Subtropical Agriculture, the Chinese Academy of Science. Isotope ratios are expressed in delta notation (δ) as

$$\delta D = \left[\frac{R_{sample}}{R_{standard}} - 1\right] * 1000 \tag{1}$$

$$\delta^{18}O = \left[\frac{R_{sample}}{R_{standard}} - 1\right] * 1000 \tag{2}$$

where R_{sample} and $R_{standard}$ are the D/H and ${}^{18}\text{O}/{}^{16}\text{O}$ ratios of the sample and the mean ocean water (SMOW) standard, respectively. The standard deviation for repeat measurement was \pm 0.3‰.

2.4. The water budget model

The central assumption of the modeling approach is that all plants on the same outcrop use only two water sources: groundwater and wellmixed precipitation stored in the cracks and crevices of the outcrop, but in variable ratios. To constrain the isotopic composition of stored rainwater with known precipitation volumes and isotope ratios, we also developed a very simple water budget model to simulate a time series of stored water volume and isotopic composition based on water input, output and evaporative enrichment. The unknown parameters of the model, regulating evaporation (E) and evapotranspiration (ET) out of the outcrop were fitted to minimize the error between observed and predicted stem water isotope ratios.

The volume of water stored in a rocky outcrop (*V*, mm) is updated daily by subtracting daily evapotranspiration (*ET*, mm) out of this pool and adding daily precipitation (*P*, mm):

$$V(t+1) = V(t) - ET(t) + P(t)$$
(3)

However, water stored in the epikarst cannot exceed a limit V_{max} and cannot be smaller than zero and is reset accordingly when these limits are breached.

Evapotranspiration out of the outcrop may often be limited by the amount of rainwater stored, but cannot be higher than potential *ET*, *PET*(*t*). Following Rodriguez-Iturbe (2000), we make the simplifying assumption that there is a threshold V_1 , below which *ET*(*t*) declines linearly with plant-available water:

$$if \ V(t) \le V_1: \ ET(t) = \frac{V(t)}{V_1} PET(t)$$

$$else \qquad ET(t) = PET(t)$$
(4)

The faction of evaporation (E(t), mm) to ET(t) is assumed to increase linearly with the amount of stored rainwater:

$$E(t) = (\varepsilon + sV)ET(t)$$
(5)

The partitioning of ET into transpiration and evaporation is acknowledged to be one of the greatest challenges in hydrology (Kool et al., 2014) and not the goal of our study. The ratio of E/ET varies dayby-day and by season (Scott and Biederman, 2017; Soubie et al., 2016). Since we were only interested here in the comparatively slow effect of evaporative enrichment on water stored in the epikarst, we did not expect day-by-day variation in to be critical. However, we did consider that seasonal variation in water stored near the surface could change the proportion of E in ET and modeled the ratio accordingly as a linear function of V.

The change in isotope ratio due to evaporation is calculated before new precipitation is added. We model evaporative enrichment using a simplified Craig-Gordon model, following the procedure described by Benettin et al. (2018), with E(t)/V as the evaporation fraction. To calculate the equilibrium fractionation factors for hydrogen and oxygen, we used average daily air temperature from the nearby weather station in the empirical formula given by Horita and Wesolowski (1994). We furthermore assumed that the isotopic composition of atmospheric vapor was in equilibrium with currently stored rainwater, which is the common approximation in the absence of data (Gibson et al., 2008). To estimate the kinetic fractionation factor, we assumed that evaporation occurred 'from a small water body' ($\Theta = 1$) transport of water vapor was fully turbulent (n = 0.5), envisioning that evaporation predominantly occurred from standing water in epikarst fractures. This also produced greater prediction accuracy. New precipitation with isotope ratios δD_{rain} and δ^{18}_{Orain} mix with the water that remains at the end of the day to give the new isotope ratios for stored rainwater:

$$\delta D(t+1) = \frac{\delta D_{enriched}(t) * (V(t) - ET(t)) + \delta D_{rain} * P(t)}{V(t) - ET(t) + P(t)} \tag{6}$$

$$\delta^{18}O(t+1) = \frac{\delta^{18}O_{enriched}(t) * (V(t) - ET(t)) + \delta^{18}O_{rain} * P(t)}{V(t) - ET(t) + P(t)}$$
(7)

At any point in time, individual plants of species x take up a proportion $f_x(t)$ of groundwater and $(1 - f_x(t))$ of stored rainwater, which through mixing results in the plant isotope ratios of:

$$D_x(t) = (1 - f_x(t)) * \delta D(t) + f_x(t) * \delta D_{ground}$$
(8)

$$\delta^{18}O_x(t) = (1 - f_x(t)) * \delta^{18}O(t) + f_x(t) * \delta^{18}O_{ground}$$
⁽⁹⁾

The isotope ratios of groundwater were taken to be constant over the simulation interval. Water samples taken from springs fluctuated between -50 and -40% for δD and between -8 and -6% for $\delta^{18}O$, with the extremes being recorded just after heavy rainfall events and likely reflecting the mixing of precipitation into spring flow. We used median spring water isotope ratios to estimate the isotope ratio of the 'pure' groundwater pool, which was -43.9% for δD and -6.8% for $\delta^{18}O$. The proportional uptake of groundwater may vary over time. Many studies have shown that reduced availability of shallow water during drought periods can drive increased groundwater uptake (Dawson and Pate, 1996; Nie et al., 2011; Quesada et al., 2008; Voltas et al., 2015; Zencich et al., 2002). We apply a simple linear approximation to encapsulate this relationship:

$$f_x(t) = a_x + b_x V(t) \tag{10}$$

Apart from the species-specific parameters a_x and b_x , this set of equations has only four unknowns: the threshold V_1 that regulates water loss from the outcrop by ET, the parameters governing the proportion of *E* in *ET*, *eand s* and the storage capacity of the outcrop V_{max} .

Table 1

Ranges and Solutions for the Hydrological Parameters of the Simulation Model. Values for Outcrops 1 and 2 were derived independently.

Symbol	Meaning	Initial range	Value Outcrop 1	Value Outcrop 2
e s	Fixed fraction of <i>E</i> in <i>ET</i> Slope of E/ET with <i>V</i>	0.0-0.50	0.00038	0.1400 - 0.00071
α	Fractionation constant for hydrogen	0.5–1.0	0.951	0.887
β	Fractionation constant for oxygen	0.5–1.0	0.973	0.944
<i>V</i> ₁	Volume threshold below which <i>ET</i> becomes water limited	0–500 mm	94	130

2.5. Parameter estimation

The objective was to find parameter values that minimized the sum of squares for the difference between predicted and observed stem water isotope ratios. The two outcrops were parametrized separately, but parameters were optimized to minimize the prediction error for all plants and sampling dates on an outcrop simultaneously.

We initialized the simulation without stored rainwater on the first day of 2014 (a day in the middle of the dry season). Since the first stem water samples were collected in mid-April 2014, the model had more than 100 days in run-up time, which proved to be enough for achieving a close fit starting with the first round of samples.

Random combinations of parameter values were picked from initially wide ranges (Table 1) to produce a 635-day time series of the volume and isotope ratio of stored rainwater. For each combination, we extracted a vector of values that corresponded to the days that stem samples were taken. Using only those values, we systematically searched for the combination of a_x and b_x values (Eq. (10)) that minimized the sum of squared differences between actual and predicted stem water isotope ratios (i.e., the SSE) across all plant samples and for both hydrogen and oxygen isotope ratios.

With only four parameter values used in the water budget model, the optimization algorithm converged quickly after a few thousand interactions. The optimization procedure was implemented in Microsoft Visual C++ 2015 Express Edition (available upon request).

Rather than reporting indicators for the overall goodness of fit, we present p values and standard errors of parameters a_x and b_x , as well as R^2 values separately for species and outcrop. These statistical parameters were calculated by multivariate regression analysis in SPSS (Version 23. Armonk, NY: IBM Corp.). Specifically, the regression model was

$$y_x = a_x \Delta + b_x V \Delta \tag{11}$$

where y_x is the difference in the δD or $\delta^{18}O$ values between species x stem samples and the stored rainwater pool (as estimated by the model), Δ is the difference in the in the δD or $\delta^{18}O$ values between stored rainwater and groundwater, V is the volume of stored rainwater (as estimated by the model) and a_x and b_x are the same parameters as in Eq. (10). Eq. (11) was derived from substituting Eq. (10) into Eqs. (8) and (9) and substituting the raw isotope ratios with the permille difference to the isotope ratio of groundwater. We emphasize that the a_x and b_x values obtained by the global optimization and by species-specific regression analysis were in fact the same, since the global optimization included the minimization of the sum of squared errors of prediction for all species individually.

To compare average groundwater use proportions between species we also evaluated the univariate regression model

$$y_x = p_x \Delta \tag{12}$$

and compared p_x values by two-sample t-tests.

3. Results

From January to December, the study area received 1247 mm in 2014 and 1681 mm in 2015. About 60% of precipitation was received in the wet season from May to September. The isotope ratios of rainwater varied seasonally with more negative values during the wet seasons and less negative or positive values during the dry seasons (Fig. 2). There was also considerable variation between rainfall events within season. Air temperatures varied between roughly 5 in January and 30 °C in July and August.

The local meteoric water line (LMWL) fell slightly above the global line, with an offset of 13 instead of 11 (Rozanski et al., 1993) (Fig. 3).



Fig. 2. Climate data from 1 January 2014 to 30 September 2015, the month that the last stem sample was taken. Bars for precipitation, closed and open circle symbols for δD_{rain} , $\delta^{18}O_{rain}$, respectively and the line for average daily air temperature. The short thick line indicates the period for which precipitation was withheld on Outcrop 1.



Fig. 3. Hydrogen and oxygen isotope ratios in precipitation and plant samples.

After removing three outliers, water extracted from all stem samples plotted below the LMWL and Outcrop 1 had noticeably more enriched samples than Outcrop 2.

The water balance parameters of the optimized simulation model are shown in Table 1, along with their initial ranges. The procedure generated apparently distinct solutions for the two outcrops, resulting in a larger amount of stored water on Outcrop 2 and a greater average daily ratio of evaporation to stored rainwater, 0.29% compared to 0.25% on Outcrop 1. The overall effect was to render the isotope ratio of stored rainwater on Outcrop 2 less responsive (more buffered) to rainfall input (Fig. A3).

The estimated proportions of groundwater use varied among species between a low of 14% for Pllo on Outcrop 2 and a high of 62% for Saro on Outcrop 1 (Table 2). The fit between predicted and observed values fell on a range of R^2 values but was no lower than 0.7.

Groundwater use proportions were statistically well separated and we may characterize them as falling into 3 groups; species with groundwater proportions of $\leq 30\%$ (Cebi and Didu on Outcrop 1, Pahe and Pllo on Outcrop 2), those with intermediate groundwater use of 31–50% (Pito on Outcrop 1, Cebi, Didu and Rasi Outcrop2) and those with use proportions well above 50% (Rasi, Saro and Steu on Outcrop 1). Two species that occurred on both outcrops had significantly higher groundwater use proportions on Outcrop 2 (Cebi and Didu), but groundwater use was a lower for Rasi on Outcrop 2. Overall, there was lower groundwater use by trees on Outcrop 2.

In six out of eleven cases, groundwater use was significantly negatively affected by the predicted amount of stored rainwater (i.e., parameter b_x had negative sign), meaning that proportional groundwater use declined as stored rainwater increased. In two cases, the effect was significantly positive. Closer inspection revealed that the positive effect may have been an artefact produced by stem water isotope ratios being close to the isotope ratio of groundwater but slightly more enriched than either of the two water sources, at a time when rainwater storage was very low. Thus, evaporative enrichment in inside stems under low flow conditions may interfere with the estimation of groundwater use trends (Klöcking and Haberlandt, 2002; Schmidt et al., 2011).

Although no plant samples were taken during the winter dry season to verify, the model predicted greater isotopic differences between stem water and stored rainwater during these times, for two reasons: First, rainwater is more enriched in the dry season and more different from groundwater (Fig. 2). Second, there is less rainwater stored in the epikarst for plants to take up. Thus, if plants were transpiring at all (only the evergreens), the model predicted that they would be using more groundwater.

4. Discussion

4.1. Species differences

The groundwater use proportions were statistically well differentiated among species between the averages of 14% and 62% (Table 2). Ground water use proportions of this magnitude have been documented for species in many other ecosystems, both in karst (Gu et al., 2015; Kukowski et al., 2013; Querejeta et al., 2007; Rong et al., 2011; Schwinning, 2008) and non-karst regions (Beyer et al., 2016; Ehleringer et al., 1991; Leng et al., 2013; West et al., 2007). It is often understood to be a component of ecological niche separation (Peñuelas et al., 2011; Silvertown et al., 2015) and indicative of enhanced to ecosystem function (Lang et al., 2014).

The differentiation of water use between vegetation components, for example between herbaceous and woody plants, is critical to the representation of ecohydrological processes (Guswa et al., 2002). Naturally, there has been a strong interest to extend generalizations to different classes of woody plants, for example to deciduous v. evergreen plants, shrub v. trees (Peek et al., 2005; Querejeta et al., 2007; West et al., 2012). Research to date has not supported such generalizations, however. For example, in one study conducted on the Yucatan peninsula, also a karst region, six species of woody plants used different water sources irrespective of whether plants were evergreen or deciduous (Querejeta et al., 2007). In a study conducted in the Brazilian cerrado, Rossatto et al. (2012) documented differences in the water sources of grasses, herbs and trees, but found none between evergreen and deciduous trees.

In our study too, the degree of groundwater use did not correlate with the usual woody plant classifications. The evergreen or semi-deciduous species Didu, Pito, Rasi and Steu had groundwater uptake proportions between 30 and 58%, and the deciduous species Cebi, Pahe

Table 2

Estimated Groundwater Proportions in the Study Species. Shown are the average proportions and the parameters a_x and b_x , provided the latter was significant (p < 0.05). The numbers in brackets are standard errors. R^2 values refer to the model fit for all samples of one species on a given outcrop and includes both δD and $\delta^{18}O$ values. Average groundwater use proportions p_x are compared between species and different letter symbols denote significant differences at the p = 0.05 level as determined by two-sample t-tests.

Species	Outcrop 1				Outcrop2			
	Average f_x	a _x	b_x	R ²	Average f_x	a _x	b_x	\mathbb{R}^2
Cebi	0.251 (0.025) ^a	-	-	0.963	0.441 (0.038) ^g	0.886 (0.070)	-0.00166 (0.00030)	0.713
Didu	0.310 (0.027) ^b	-	-	0.928	0.467 (0.042) ^h	0.900 (0.077)	-0.00210 (0.00033)	0.706
Pahe	-	-	-		0.368 (0.034) ⁱ	-	-	0.597
Pito	0.359 (0.027) ^c	0.493 (0061)	-0.00061 (0.00025)	0.829	-			
Pllo	-		-		0.304 (0.044) ^j	0.776 (0.078)	-0.00226 (0.00033)	0.588
Rasi	0.588 (0.025) ^d	-	-	0.842	0.466 (0.026) ^h	0.482 (0.061)	-0.00007 (0.00025)	0.795
Saro	0.626 (0.021) ^e	0.747 (0.046)	-0.00055 (0.00019)	0.822	-	-		
Steu	0.571 (0.048) ^f	0.362 (0.080)	0.00109 (0.00035)	0.791	-	-		-



Fig. 4. Simulated and actual δD values for all species on both outcrops. Gray line: Simulated daily δD values of stored rainwater. Thin black line: Simulated δD values of stem water for that species. Symbols: Actual δD values of stem water with different symbols for individual plants. Text in each figure indicates species, location and the estimated proportional groundwater use.

and Pllo and Saro had proportions between 14 and 62%. Of the two tallest trees, one had intermediate groundwater use (Rasi) and the other had the highest groundwater use of all the eight species observed (Saro). The tallest species had the highest groundwater use (Saro and Steu), except Pllo, which had the lowest groundwater use (Tables 1 and 2). However, Saro and Steu, had by far the largest leaves and low wood densities, suggesting a high transpiration and growth capacity and relatively low drought tolerance (Gleason et al., 2016). Both species are shallow-soil endemics (He et al., 2012; Huang et al., 2014; Wang et al., 1998), which are often characterized by strong tap root development

(Nie et al., 2014; Poot and Lambers, 2008; Renton and Poot, 2014). Thus, leaf and wood characteristics may be better indicators of groundwater use, as they signal adaptation to consistently high water-availability.

The study also found apparent differences in plasticity of water source utilization in some species. The species Cebi, Didu and Pllo on Outcrop 2 displayed the strongest tendencies to increase groundwater use as stored rainwater ran low, while Pahe exhibited none (Table 2, Fig. 4) There are many examples of woody plant species substituting shallow with deeper water for transpiration during drought, especially in seasonally-dry ecosystems (Evaristo et al., 2016; Nie et al., 2011). The degree of water source plasticity is either adaptive or site-dependent (Ehleringer and Dawson, 1992; Williams and Ehleringer, 2000). As an adaptation, the ability to 'switch' between water sources has costs, one of which is the cost of maintaining a dimorphic root system consisting both shallow and deep tap roots (Torres et al., 2002). This investment may simply not pay off for all species in a community. In karst regions especially it is also quite likely that root access to groundwater varies from site to site and from tree to tree, since the degree and pattern of rock fracturing can vary greatly across space (Hu et al., 2015; Tokumoto et al., 2014; Yang et al., 2016) and root development through fractured rock could be highly individualistic. This may explain why all the three species that occurred on both outcrops differed significantly in groundwater use proportions.

Despite the variability between individual trees documented in Fig. 4, the analysis highlighted significant differences between species in ground water use. This is all the more remarkable because the species were members of a small community confined by the limited space of an outcrop rising above a mountain slope. In general, the South China Karst has high tree diversity (Li et al., 2013). This study suggests that even just one specific element of the karst landscape, the rocky outcrop, has the capacity to support several species with contrasting water use.

4.2. Evaluation of the measurement and analysis method

We tested an alternative analysis method for plant and water isotope data to overcome the sampling limitations of rock-dominated ecosystems. The method was based on estimating, rather than sampling, the isotope composition of stored rainwater. In the absence of known values for the parameters of a water budget model, we used repeatedly measured plant water isotope ratios to constrain the parameters of the model. The four parameter values that governed the water budget model produced unique optima on both outcrops that minimized the sum of square errors of the prediction (Fig. A2). Two more parameters were used to describe the groundwater use for each individual species. The fit of individual species' stem water isotope ratios to the two-source model was generally good and produced significant parameter estimates.

To some extent, the overall good fit between the data and the model is expected, given that model parameters were based on minimizing prediction error. On the other hand, we could not take for granted *a priori* that one simulated time series would necessarily fit all species on one outcrop reasonably well (Fig. 4). For example, the existence of a theoretical third, independently varying water source, used by some but not all species could have produced inexplicable variation and worsened the model fit.

However, the fit for the $\delta^{18}O$ data was visibly worse than for the δD data (Fig. A4). In part this stems from the optimization procedure, which was weighted towards fitting the δD values, which had much greater spread. While we could have given prediction errors equal weighting, we decided not to do so over concerns that oxygen could have been fractionated by processes other than evaporation. It is well documented that oxygen in water can exchange with the oxygen in the calcium carbonate of clay materials that are typically lodged at the bottom fractures (Meißner et al., 2014; Newberry et al., 2017; Oerter et al., 2014). This exchange could have buffered variation in oxygen isotope ratios relative to variation in δD . Some researchers prefer not to use oxygen isotopes in water sourcing for this reason (Hu et al., 2015; Sprenger et al., 2015; Yang et al., 2016), but we decided to use both elements since the estimated groundwater use values were consistent between fitting the model only with only δD versus both δD and $\delta^{18}O$ values.

Two periods appeared to produce greater discrepancy between observed and modeled δD values (Fig. 4). One occurred on Outcrop 1 in August 2015. This was the period in which the outcrop was covered by a plastic sheet to exclude rain. By comparison, Outcrop 2, which was not covered, showed less discrepancy with the model prediction over the same period. It is highly probable that the cover was not 100% effective in excluding rain, so that trees on Outcrop 1 received unequal quantities of rainwater input. Rainfall δ D values during this time ranged from -30 to -70% and most stem water δ D values also fell into this range. Related to this observation, we consider the rainfall manipulation experiment to have been ineffective and omit further discussion of the third goal of the study, accordingly.

On Outcrop 2, the first stem samples collected in 2015 were far from the predicted isotope ratio of stem water and groundwater, but generally similar to the last recorded stem water isotope ratios from the previous year. It seems likely that plants had not yet begun to take up water. But it is notable that plants on Outcrop 1 did not display this discrepancy, this discrepancy on Outcrop 2 might be related to the phenologically delay (by personal observation).

An alternative analysis approach for rocky habitats had previously been introduced by Nie and coworkers (Nie et al., 2011; Nie et al., 2012). In it, the elusive isotope composition of stored rainwater was approximated as the running average for antecedent rainwater, thus assuming no evaporative enrichment. This method was successful in terms of demonstrating the water use diversity of karst species, but groundwater use proportions could only be considered rough estimates, due to uncertainties associated with averaging the isotope ratios of antecedent rainwater. And although evaporative enrichment had a relatively small influence on stored rainwater in the present model, it was still significant in producing a better fit. Ignoring enrichment would have systematically biased groundwater use estimates.

Furthermore, the approach we used here is a departure from the 'snap shot' approach, which seeks to interpret stem water isotope data separately for each sampling date and species. Instead, we analyzed the entire two-season data set jointly on the assumption that at any time, all species have access to the same two water sources and within species there is continuity in groundwater uptake, i.e., no sudden changes in groundwater consumption are expected. This diminishes the problem of lack of isotopic separation between water sources, which may occur by chance on one sampling date, but not repeatedly, given the variability in the isotope ratios of precipitation. Overall, we believe that this approach can yield more robust estimates of seasonally integrated groundwater use, provided the two-source approximation is justified.

In general, it is challenging to estimate the proportional use of water sources through isotope tracer techniques. Even where soil samples can be taken, the isotope ratios of near-surface water sources are highly variable in space due to uneven infiltration and shading, differences in soil temperature and many other environmental factors that influence isotope fractionation. This variability is integrated to some extent by the plants themselves, since they take up water from a large soil volume across this heterogeneity. Individual plant values are further integrated by sampling multiple individuals to obtain a 'population' average. Here we have taken one step further by assuming there is an integrated community average of near-surface soil water that all members of the community use to varying degrees.

The new analysis method may be applicable to other environments. It helps to have a relatively simple structure of plant-available water pools and transparent recharge processes. Beyond this, more complex models (Rothfuss and Javaux, 2017; Sprenger et al., 2016) could conceivably be parameterized in part by optimizing the fit with observed stem sample isotope ratios, as was done here. The key is the triangulation of dominant plant water sources through the joint analysis of stem water isotope ratios across the species of a community, as opposed to developing separate models for each species.

5. Conclusion

Species-rich plant communities are typically composed of many species with contrasting water use patterns that vary through time and space. The methods currently employed to examine plant water sources are too costly and time-consuming to adequately integrate plant water use at the landscape level, a critical need for advancing the study of Earth's critical zone. We developed and tested a greatly simplified sampling and analysis protocol, which produced well differentiated estimates of proportional groundwater use for eight species over two growing seasons. Whether it can be extended to other ecosystems is a matter of future examination. However, insights derived from the application of static ('snapshot') mixing models may have already reached their potential. Novel approaches are now needed that couple isotope data to dynamic process models.

The South China karst is in desperate need of guidelines for forest restoration. The recovery of critical ecosystem services such as flood control requires knowledge of species' interactions with the hydrological cycle. Our results suggest that woody plants growing on rocky outcrops vary greatly in proportional groundwater use. Preference in initial restoration should be placed on fast-growing species that use the greatest amount of groundwater. Over the long run, a diverse community containing a spectrum of water use patterns is the end goal.

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