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Tropical forest water source patterns revealed by stable isotopes: A preliminary analysis of 46 neighboring species

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ABSTRACT

Stable isotope tracing of plant water use can illuminate plant water sources. But to date, the number of species tested at any given site has been minimal. Here, we sample 46 tropical hardwood tree species in a 0.32 ha plot with uniform soils. Soil water was characterized at 6 depths at 0.2 m intervals down to 1 m and showed simple and predictable depth patterns of δ^2 H and δ^{18} O, and simple and spatially uniform isotope composition at each depth. Nevertheless, tree xylem water δ^2 H and δ^{18} O showed remarkable variation covering the full range of soil composition, suggesting strong sorting and niche segregation across the small plot. Wood density, tree size and mean basal area increment together explained approximately 55% of the variance of xylem water isotope composition from the middle portion of the soil profile. The majority of the observed species relied on 0.0–0.2 m depth soil water. This layer contributed approximately 75% of the xylem water which was significantly higher than the contributions from all other depths. The contribution from shallow soil was highest for trees with high wood density, slow-growing trees and small-sized trees. Our work suggests that stable isotope tracers may aid a better understanding of tropical forest water uptake depths and their relation to tree functional traits and potential hydrological niche segregation among co-occurring tropical species.

1. Introduction

Water uptake patterns across diverse tropical rainforest tree species are poorly known (Goldsmith et al., 2012). This is because such patterns are difficult to measure and that tree root distributions are extremely difficult to quantify (Kleidon & Heimann, 1998). In the past decades, studies have begun to sample the stable isotope composition (δ^2 H and δ^{18} O) of soil water and plant xylem water to quantify tree water uptake depths (Brooks et al., 2010). Most site-based work in the tropics has employed a single isotope approach (i.e. using either δ^2 H or δ^{18} O) to quantify the depth in the soil profile where trees source their soil water or groundwater (Jolly & Walker, 1996; Meinzer et al., 1999; Slavich et al., 1999; Sekiya & Yano, 2002; Atsuko et al., 2002; Peñuelas & Filella, 2003; McCole & Stern, 2007). Recent investigations using dual isotopes have shown that soil source water can often plot below the meteoric water line (MWL)¹. As such, δ^{2} H and δ^{18} O can give two different source depths. But when used together, this dual isotope approach can help quantify not only water update depth, but differentiate between rainfall, soil water and groundwater in ways not possible with the single isotope approach (Evaristo et al., 2015). To date, only a limited number of studies have used the dual isotope approach to quantify plant water uptake depth in the tropics (e.g. Querejeta et al., 2007; Goldsmith et al., 2012; Schwendenmann et al., 2015; Evaristo et al., 2016).

Here we examine the differences in water uptake depth for 49 individual trees from 46 species in a 0.32 ha (20×160 m) experimental plot

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¹ The Meteoric Water Line (MWL), is a regression line which is derived from precipitation water isotope data (δD and $\delta^{18}O$) (Craig, 1961). The MWL can be for a single site, where it is called a "Local Meteoric Water Line (KMWL)" or from across the globe where it is known as the "Global Meteoric Water Line (GMWL)".



Fig. 1. (a) Location of the study area within Australia. Green color in the inset map indicates wet tropical rainforest. The red dot indicates the location of the studied permanent plot in the tropical rainforest area (b) The light green dot indicates location of the plot in high resolution (c) Aerial view about the plot location. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

located in a wet tropical rainforest in north Queensland, Australia. Our null hypothesis is that diverse tropical hardwood species show the same xylem water isotope composition and hence the same depths of soil water extraction. We use a dual isotope approach to trace soil water uptake and a Bayesian mixing model (following Evaristo et al., 2017) to quantify water uptake depth for each tree. Past work using mixing models and dual isotope data in the tropics has shown differing water sources for a single species during wet and dry seasons (e.g. Evaristo et al., 2016). But that work, and most other studies to date (Querejeta et al., 2007; Schwendenmann et al., 2015), have considered only a single species or a few species at best. This has limited complete understanding of tropical plant species' water uptake strategies. Beyond these dualisotope issues, the isotope approach on has only been applied to a limited number of tree species within a single plot and this has not enabled the study of plant functional traits and their potential link to water use strategies (Schuldt et al., 2011; Worbes et al., 2013).

So what do we know about plant traits and water use in the tropics? A study in seasonally dry mountain grasslands of Brazil has shown that water uptake strategies can be related to root and leaf hydraulic trait coordination, suggesting that shallow-rooted species have more drought-resistant leaf traits (Brum et al., 2017). Recent work by Brum et al. (2019) in the Amazon rainforest has shown that water use is related to rooting depth, water potential tolerance and light conditions. Physiological studies have shown that rooting depth or the phenology of trees can lead to spatial and temporal partitioning of limiting resources, such as water (Schwinning & Ehleringer, 2001). Indeed, a recent study modelled species-level hydrological niches in response to drought, showing how water availability can be experienced differently by tree species in a forest (Chitra-Tarak et al., 2017).

water uptake strategies and depths. Bennett et al. (2015) have shown that during drought, large trees suffer most in forests across the globe. However, there are other studies showing that small trees are more prone to mortality than large trees (Lorimer et al., 2001; van Mantgem et al., 2009; Peng et al., 2011; Zhang et al., 2015). In general, larger trees have greater access to deep soil water during drought because of their deeper root systems (Horton and Hart, 1998). This means large trees may be less susceptible to decline or mortality during drought. However, there are some exceptions to this rule because some large trees lack a deep root system (Mueller et al., 2005; Anderson-Teixeira et al., 2015). For example, Romero-Saltos et al. (2005) found that large-diameter trees uptake water from deep in the soil profile. In contrast, Meinzer et al. (1999) observed that during dry periods, small-diameter trees withdrew more water from deep soil layers than large-diameter trees.

Here we use an exceptionally species-rich tropical plot-the largest in a single plot studied to date using the isotope method that we are aware of-to advance our understanding of tropical rainforest tree water uptake depth patterns and differences in morphological traits among neighbouring species. We investigated the depths where large and small trees across our plot uptake water to help improve our understanding of the water use strategies across different tree species and sizes. In addition, we explore if variation in the use of water resources is related to the differences in growth and survival rates between co-ocurring trees. We used the long-term dataset to identify trees with different growth rates and investigate the soil depths from which those trees are taking up water, aiming additionally at improving our understanding of how access to soil water influences rainforest tree productivity. We examine wood density across our site since it has been shown to be negatively correlated to growth and mortality rate (Poorter et al., 2008, Nguyen et al., 2014a). Wood density has also been shown to be negatively

Beyond traits, tree size is another factor for potential variation in

Table 1
Traits of the sampled woody tree species.

Tree ID	Speciesname	DBH (cm)	Family	Leaf Phenology	Growth form	Successional status	Phylogenetic Group	Leaf type	Photosynthetic Pathway	Leaf compoundness	Wood density (g/cm ³)	MBAI (cm ²)
0	Agathis atropurpurea	11.3	Araucariaceae	Е	F	ES	G	В	C3	S	0.413	N/A
1	Agathis robusta	32.6	Araucariaceae	Е	М	LS	G	В	C3	S	0.401	0.0012
2	Alangiumvillosum	11.9	Cornaceae	E	M	LS	AE	В	C3	S	0.607	0.0001
3	Aleuritesmoluccana	44.1	Euphorbiaceae	E	F	ES	AE	В	C3	s	0.400	0.0019
4	Aleuritesmoluccana	47.4	Euphorbiaceae	E	F	ES	AE	В	C3	S	0.400	0.0019
5	Alloxylonwickhamii	42.8	Proteaceae	E	M	LS	AE	В	C3	S	0.456	0.0016
6	Anthocarapanitidula	15.6	Meliaceae	F	M	LS	AF	B	C3	C	0.689	0.0002
7	Anhananthenhilippinensis	18.2	Ulmaceae	F	M	LS	AF	B	C3	S	0.620	0.0002
8	Arovrodendronneralatum	30.4	Malvaceae	F	S	M	AF	B	C3	C	0.810	0.0010
9	Argyrodendrontrifoliolatum	20.5	Sterculiaceae	F	S	M	AF	B	C3	C	0.800	0.0005
10	Arovrodendrontrifoliolatum	16.3	Sterculiaceae	F	s	M	AF	B	C3	C	0.800	0.0001
11	Aryteradivaricata	13.7	Sanindaceae	F	м	IS	AF	B	C3	C	0.633	0.0001
12	Castanospermumaustrale	14 5	Fabaceae	F	M	LS	AF	B	C3	C	0.650	0.0013
12	Castanosporaalphandii	12.2	Sanindaceae	F	M	IS	ΔE	B	C3	C	0.607	0.0001
14	Celtispaniculata	60.5	Ulmaceae	D	M	IS	ΔE	B	C3	s	0.607	0.0041
15	Conspanicalia	18.0	Lauraceae	F	S	M	AM	B	C3	s	0.650	0.0041
15	Daphnandrarapandula	17.4	Atherospermataceae	E	S	M	AM	B	C3	S	0.030	0.0004
10	Departmentaria arepartanta	30.0	Urticaceae	F	VE	D	AF	B	C3	S	0.301	0.0001
19	Diospuros hebecarna	22.0	Ebenaceae	E	S	M	N/A	B	C3	C C	0.207	N/A
10	Diospyros nebecurpu Dinloglottisdinbyllostagia	137	Sopindoceoe	E	M	IS	N/A AE	B	C3	C	0.754	N/A
20	Doputorisaiphyliostegia	10.2	Atherospermataceae	E	E	ES	AM	B	C3	c c	0.734	0.0003
20	Duryphoraaronnaaica	10.5	Moliogono	E	г	ES LC	AIVI	D	C3	3	0.462	0.0003
21	Dysoxytumoppositijotum	19.0	Mellaceae	E	N		AE	D	C3	C	0.736	0.0001
22	Elassamus mandia	13.0	Flagger	E	IVI NA	LS LS	AE	D	C3	C C	0.033	0.0001
23	Elaeocarpus granais	35.5	Liaeocarpaceae	E	M	LS M	AL	В	C3	5	0.495	0.0018
24	Enalanaralongipealcellala	45.7	Lauraceae	E	5	M	AM	D	C3	8	0.839	0.0004
25	Ficus spp.	13.8	Moraceae	E	IVI E	LS EC	AE	D	C3	8	0.390	0.0005
20	Ficustuspida	1/./	Moraceae	E	F	ES	AE	D	0	5	0.415	N/A
2/	Ficusieptociada Flim denni no de attinue	18.5	Moraceae	E	F	ES LC	AE	В	C3	8	0.482	0.0003
28	Flinderslaschottland	22.1	Rutaceae	E	M	LS	AE	В	C3	L A	0.581	0.0005
29	Glochialonferainanai	12.6	Phyllanthaceae	E	F	ES	AE	В	C3	8	0.593	0.0001
30	Gmelina fasciculifiora	57.3	Lamiaceae	E	S	M	AE	В	C3	S	0.470	0.0008
31	Homaliumcircumpinnatum	20.7	Flacourtiaceae	E	M	LS D	AE	В	C3	8	0.788	0.0006
32	Mallotusphilippensis	11.4	Euphorbiaceae	E	VF	P	AE	В	C3	S	0.650	0.0009
33	Mallotuspolyadenos	14.0	Euphorbiaceae	E	VF	P	AE	В	C3	S	0.650	0.0002
34	Memecylonpauciflorum	11.6	Memecylaceae	E	F	ES	AE	В	C3	s	0.808	0.0001
35	Mischocarpus pyriformis	16.7	Sapindaceae	E	M	LS	AE	В	C3	C	0.805	0.0004
36	Myristicainsipida	16.0	Myristicaceae	E	S	M	AM	В	C3	S	0.482	0.0003
37	Myristicainsipida	10.4	Myristicaceae	E	S	M	AM	В	C3	S	0.482	0.0003
38	Phaleriaclerodendron	11.5	Thymelaeaceae	E	M	LS	AE	В	C3	S	N/A	0.0001
39	Polyscias elegans	42.3	Araliaceae	E	F	ES	AE	В	C3	C	0.410	0.0023
40	Pouteriaobovoidea	49.4	Sapotaceae	E	M	LS	AE	В	C3	S	0.630	N/A
41	Pouteriaxerocarpa	14.1	Sapotaceae	E	М	LS	AE	В	C3	S	0.607	0.0006
42	Pseudoweinmannialachnocarpa	18.3	Cunoniaceae	E	М	LS	AE	В	C3	С	0.758	N/A
43	Stenocarpussinuatus	16.0	Proteaceae	E	М	LS	AE	В	C3	S	0.629	0.0003
44	Streblusbrunonianus	21.2	Moraceae	E	Μ	LS	AE	В	C3	S	0.702	0.0001
45	Syzygiumclaviflorum	11.1	Myrtaceae	E	S	Μ	AE	В	C3	S	0.607	N/A
46	Terminalia sericocarpa	33.9	Combretaceae	E	Μ	LS	AE	В	C3	S	0.640	0.0016
47	Toonaciliata	31.8	Meliaceae	D	Μ	LS	AE	В	C3	С	0.383	0.0014
48	Zanthoxylum ovalifolium	12.0	Rutaceae	E	Μ	LS	AE	В	C3	С	0.610	N/A

N.B. Leaf phenology: E- Evergreen, D- Deciduous, Growth form: VF-Very fast, M-Moderate, F-Fast, S-Slow; Successional status: LS-Late secondary, ES-Early secondary, M-Mature, P-Pioneer; Phylogenetic Group: AM-Angiosperm Magnoliid, AE-Angiosperm Eudicotyl, N/A-Not available, G-Gymnosperm; Leaf Type: B-Broadleaved; Leaf compound ness: C-Compound leaf, S-Simple leaf.



Fig. 2. The spatial distribution of all the studied tree species throughout the 20×160 m plot. Different sizes of the green circles indicate DBH differences among the trees. The whole plot was then divided into a 10×10 m grid. The codes outside of the grid indicate the grid ID. The black circles in each grid indicate the bore-hole location for soil sample collection. The numbers within the grid represent the tree species ID. Details for each tree can be found in Table 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

correlated to stem water storage capacity (Oliva Carrasco et al., 2015) which can act as a buffer during drought (Pineda-García et al., 2013). Together, this will also help in identifying complementary tree species to design mixed-species plantations (e.g. Nguyen et al., 2014b) that can make better use of water resources in the era of climate change. By leveraging this large species assemblage on a relatively flat plot, we explore the following research questions:

- 1. What are the water uptake depths across 46 species within a 0.32 ha forest plot?
- 2. How do tree functional traits relate to water uptake depth?

2. Materials and methods

2.1. Experimental site and studied species

The study site was located in a wet tropical rainforest in the Danbulla state forest on the Atherton Tableland in north eastern Australia (Fig. 1). The site has an elevation of 760 m above sea level (Drake & Franks, 2003). Trees were located within a long-term experimental plot (referred to as "Experiment 78, Plot 2") established by the Queensland Department of Forestry in 1948, with regular measures of the growth, mortality and recruitment of trees greater than 10 cm diameter at breast height (DBH). The plot was subjected to silvicultural treatment in 1949 consiting of thinning of non-commercial species (Wills et al., 2018). Soils on the 200 \times 20 m experimental plot were sandy clay loam to clay loam. The soils have developed from Pliocene to Holocene lava flows from volcanic eruptions (Laffan, 1988). The annual average rainfall at the site is 1680 mm, with over 1000 mm falling between December and February (Drake & Franks, 2003). The area can be prone to seasonal droughts resulting from infrequent rainfall during the drier months (Drake & Franks, 2003) and we note that a small 3–9 mm rainfall event was recorded near the study site before the sampling campaign (Supplementary Fig. 1).

2.2. Tree species characteristics

Forty-nine individual trees were sampled from a study plot that contained 46 different species (Table 1). Much of the tree functional traits information was gathered from the secondary literature: phylogenetic group (Kattge et al., 2011) and life form (Kattge et al., 2011). Successional status and growth form of each species was based on Goosem & Tucker (2013). Where species-level information about successional status was not available, genus-level information was used. Information on the species' family, leaf phenology, leaf compoundness, woodiness, life form and phylogenetic group was collected from the TRY global database of plant traits (Kattge et al., 2011). Wood density data were collected from the Global Wood Density Database (Zanne et al., 2009). If a species' wood density was not available from this global database, Queensland government data were used (https://www.daf. qld.gov.au/forestry/using-wood-and-its-benefits/wood-properties-of-t imber-trees). Data on the species growth rates were obtained from historical records associated with "Experiment 78, Plot 2" which was established in 1948 and is part of a permanent plot network established by the Queensland Department of Forestry. Tree species and diameter at breast height (DBH) were measured for all trees ≥ 10 cm DBH at regular periods dating back to 1948 to 2015. Basal area increment (BAI) was used as a proxy for tree growth. The mean annual tree growth rate was calculated as = [BA_{census2}- BA_{census1}]/[time₂-time₁]. Mean BAI (MBAI) was then calculated for each sampled species. BA was calculated using the formula BA = 0.00007854 X DBH (cm)², where BAI is defined by the change in BA between measurement periods, divided by the number of years within the measurement period (Da Cunha et al. 2016).

2.3. Plant and soil sample collection

The sample design is shown in Fig. 2. All the sampled tree species were located within the 20 \times 160 m plot. The plot was further divided into 10×10 m grids. Soil samples were collected from the centre of each of the 10×10 m grids using a 100 mm soil auger, with samples collected at 0.2 m intervals down the soil profile (i.e. at 0, 0.2, 0.4, 0.6, 0.8 and 1.0 m). All the soil samples were collected over a two-day period (22nd and 23rd July 2016). Additional soil samples were collected from 0 to 4.0 m (0, 0.2, 0.4, 0.6, 0.8, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5 and 4.0 m) down the soil profile using a truck-mounted soil auger from a location adjacent to a small access track about 60 m south of the plots on 15th July 2016. From each of the 0–1.0 m soil depth sampling locations, 400 g of soil was placed into a Ziploc® bag, placed into a refrigerator, and stored until laboratory analysis. For the additional soil depth sampling depth locations (1.0-4.0 m), samples were placed in capped vials, wrapped with parafilm, placed into a refrigerator, and stored until laboratory analysis. Gravimetric soil moisture content (%) at six depths (0, 0–0.2, 0.2–0.4, 0.4-0.6, 0.6-0.8 and 0.8-1.0 m) were measured at each soil sample location (following Klute, 1986).

Xylem samples were collected from trees using a battery-powered drill at approximately 10 cm above or below the DBH mark. Xylem samples were taken on the side of the stem facing towards the soil bore hole. All xylem samples were collected between 9 am and 3 pm on 22nd July 2016. Before collecting the samples, all the bark tissue was removed. Sufficient xylem tissue was then collected and placed immediately into 24 ml capped glass vials. To distinguish between sapwood and heartwood, a visual observation technique was applied. In general, sapwood has a lighter color than heartwood. In most cases, there was a very clear colour distinction between heartwood and sapwood. In the limited number of trees where the sapwood was difficult to distinguish, cores were taken from a shallow area (ca 5 mm) immediately under inner bark. If there was not enough sapwood from one core, a second core was taken using the same drill system. The vials were then immediately sealed and wrapped in parafilm to prevent evaporation. The xylem samples were then placed into a cooler and then refrigerated until



Fig. 3. Soil texture of the 20 × 160 m plot. The top figure represents the upper transect of the plot and the lower figure represents the lower transect of the plot.

laboratory analysis.

2.4. Water extractions

Water was extracted from the xylem samples using cryogenic vacuum distillation (Orlowski et al., 2013). The extracted water was then analyzed for δ^2 H and δ^{18} O on a Delta V Advantage mass spectrometer following Nelson (2000). Soil water from 0 to 1.0 m depth in the plot was extracted using the direct vapour equilibration method described in Orlowski et al. (2016) by placing 400 g of soil into a Ziploc® bag, with subsequent amounts of reference water (i.e. known water isotope). The Ziploc®bags were evacuated, sealed and massaged to homogenize and then placed inside a second Ziploc® bag, and stored to equilibrate prior to analysis. Soil water from the additional 1.0–4.0 m samples outside the plot was obtained through the cryogenic vaccum extraction as per Orlowski et al. (2013).

All δ^2 H and δ^{18} O values were expressed relative to Vienna Standard Mean Ocean Water (*VSMOW*) and the lab precision for δ^2 H and δ^{18} O was estimated to be +/- 1 permil and +/- 0.2 permil, respectively.

2.5. Bayesian mixing model to determine soil water proportions in xylem tissue

The MixSIAR (stable-isotope analysis in R) Bayesian mixing model statistical package (Moore & Semmens, 2008; Parnell et al., 2013; Stock & Semmens, 2016) was used to partition source water contributions to xylem tissue. MixSIAR is widely used in food web and animal foraging studies and was used in this study to determine the relative importance of various sources of water that may contribute to xylem water using Markov Chain Monte Carlo (MCMC) methods. Five potential source classes were used for xylem water when running the mixing model: (1) soil water at 0–0.2 m; 2) 0.2–1.0 m; 3) 1.0–2.0 m; 4) 2.0–3.0 m; and 5) 3.0–4.0 m as they were statistically significantly different. The source classifications are used here only to designate the soil water endmembers that can be resolved by MixSIAR. Cryogenically extracted water from 0 to 1 m soil was excluded from analysis because of possible exposure to evaporation due to sampling location outside plot on the forest edge near access track. Therefore, the model used soil water

analysed through vapour bag equilibration for the 0–1 m depths sampled inside the plot and cryogenically extracted water for the 1–4 m depths from outside the plot. To test the effect of combining soil from the different extraction methods, we ran additional model variations using different numbers of sources (depths) while including or excluding the cryogenically exctracted soil from 0 to 1 m—which overlaps with the vapour bag soil from 0 to 1 m in the plot. We were able to verify that source contribution patterns remained similar regardless of the inclusion or exclusion of the 0–1 m cryogenically extracted soil, changing only with the number of sources used. The MCMC model run was set to 'very long' (1,000,000 iterations) and the source water's estimated contribution (i.e. the median of the posterior probability distribution of the MCMC simulation) to xylem water was obtained for all the sampled trees (see supplementary Figs. 1–3).

2.6. Tree functional trait influence on water uptake depth analysis

Principal Component Analsis (PCA) was used to observe the variation in xylem isotope explained by tree traits. To investigate the influence of MBAI, tree size and wood density on soil water depth contribution to xylem, bivariate Pearson correlations were conducted. In the PCA analysis we used MBAI as a surrogate for growth. In doing so, we recognise that DBH increment is also a valid and widely used surrogate for growth. In our study the two variables were very highly correlated (r = 0.97) and the decision to use MBAI had no impact on the analysis. We included both tree Size (DBH) and MBAI (growth) as they represent traits that may affect water uptake in difference ways. We tested the impact of the decision to include both variables by running the PCA including both tree Size and MBAI and then excluding one of the variables (see Supplementary Table 1).

3. Results

3.1. Soil moisture, texture and isotopic signature

Soils across the small plot ranged from sandy loam to clay loam (Fig. 3). The upper soil layer was comprised mostly of sand and gravel together with organic matter. Root density was highest in the shallower



Fig. 4. Average soil water content difference between the (a) left (S10-S25)-right (S26-S40) and (b) upper-lower transect of the studied plot. Error bars indicate standard deviation.

parts of the soil profile. Sandy loam dominated the middle portion of the soil layer where root density was lower compared with the shallow soil layer. The deep soil layer was mostly hard clay. Few roots were observed in the deep soil layers throughout the small plot.

Fig. 4 shows that water content increased with soil depth. Water content differed significantly (ANOVA-Tukey Method, p < 0.5) among the sampled soil depths. However, moisture content was homogeneous across the plot in each layer. Water content in the top 0.5 m was 5–15% during the sampling period and soil moisture content increased with depth to a maximum of 27% (Fig. 4).

Fig. 5 shows a dual isotope plot of water extracted from each soil depth. There was a clear and predictable variation in water isotope composition with depth, with less negative signatures in the surface soil and more negative signatures with depth. Soil water isotopic signatures were relatively homogeneous for each soil layer. A one-way ANOVA with the Tukey method showed no significant difference in soil water isotope composition (p > 0.05) between the two transects' soil layers (Fig. 5).

3.2. Tree water uptake depth and source water contribution

Fig. 6 shows all xylem and soil samples in the dual isotope space. Soil water showed a consistent trend of more negative signatures with depth (Fig. 6). All the sampled soil water from 0 to 1 m in the plot (vapor bag equilibration) plotted along the Local Meteoric Water Line (LMWL), suggesting low evaporation effects in this humid rainforest setting (Fig. 6). However, soil from 1 to 4 m (cryogenically extracted) plotted below the LMWL-possibly due to extraction effects. It could also be associated with the samples collected from the forest road edge sampling location being more exposed to evaporation. However, this effect is likely to only be in the top 50 to 100 cm at most as the road construction resulted in little, if any impact, to deeper parts of the soil profile. Qualitative assessment of 41 of the 49 xylem samples suggests that these trees used mostly shallow soil water since they overlap isotopically with soil water from the 0–0.4 m depth (Fig. 6). To quantify the water uptake depths beyond the simple visual analysis, Fig. 7 (also see supplementary Table 3) shows the mixing model results for the contributions of different soil water depths to the 49 individual xylem water samples. Soil water contributions to xylem water from the 0.0-0.2 m depth at the sampled tree population level was 75.3% (median, 95% Credible Interval [0.64, 0.85]). This was significantly higher than the contributions from all other depths. Source contributions to xylem water from the 0.2–1.0 m depth were the smallest at 0.7% (0.00, 0.06), while contributions from the 1.0–2.0 m depth, the 2.0–3.0 m depth, and the deepest (3.0–4.0 m) layer were 9.8% (0.00, 0.32), 2.1% (0.00, 0.16), and 5.6% (0.00, 0.26), respectively.

3.3. Functional traits and their relation to water uptake depth

Three of the ten tree functional traits (i.e. tree size, MBAI and wood density) were used to test their relationship with soil water uptake depth. The remaining traits of all species were not different and were excluded from further analysis (Table 1).

Assessing trait-trait correlations showed that size was positively correlated to MBAI (R = 0.78, R² = 0.61*p* < 0.001), while wood density was weakly negatively correlated to size (R = -0.34, R² = 0.12, *p* = 0.03), and moderately negatively correlated to MBAI (R = -0.46, R² = 0.21, *p* < 0.01), suggesting that smaller and slower-growing trees have higher wood density. Wood density, tree size and MBAI explained 54.8% of the variation of xylem water isotope ratios (δ^2 H and δ^{18} O) composition in the first axis of the Principal Component Analysis (Fig. 8).

Wood density was significantly positively correlated (r = 0.28) with very shallow (<0.2 m) soil water contribution, indicating that with an increase in wood density, the contribution of very shallow soil (<0.2 m) increased (Table 2). All other soil layer contributions to xylem water were significantly negatively (p < 0.05) correlated with wood density except the 0.2–1 m depth, indicating that with a decrease in wood density, the contribution of deep soil (<0.2 m) increased. Both tree size and MBAI were significantly negatively correlated with very shallow (<0.2 m) soil water contribution, indicating that the smaller the tree and the lower the MBAI, the contribution of very shallow soil (<0.2 m) increased. However, size and MBAI were positively correlated with all deeper soil layers, suggesting that contributions from deep soil layer increase for larger trees and faster growing trees.



Fig. 5. (a) Dual isotope plot of the soil water isotope difference between the left (S10-S25)-right (S26-S40) proportion and (b) upper-lower transectof the experimental plot. Each plot has the Local Meteoric Water Line (LMWL) as a reference. The boxplots show the average (dashed line) of the isotope ratios, while data extremes are shown by the respective symbol. Statistical grouping is indicated by a continuous line to the left or below for δ^{18} O and δ^{2} H, respectively. A similar color line indicates no significant difference (p < 0.05) between plot proportion of the same soil depth. Soil water isotope for the 1–4 m depth is not shown here as those samples were collected outside of the plot sub-grids. Error bars indicates standard deviation.

4. Discussion

4.1. Interspecific differences in water uptake depth

We found that most of the 46 species of rainforest trees sampled relied on shallow water from the top 20 cm of the soil profile. It was striking that the 46 species sourced a low proportion of water from 0.2 to 1.0 m soil depth (Fig. 8). These patterns are in stark contrast to past research on tree water uptake depth in tropical regions using a single isotope approach which have reported that most of the studied tree species generally source soil water from depths of 0.2–1.0 m (Jackson et al., 1995; Meinzeret al., 1999; Oliveira et al., 2005; Hasselquistet al., 2010; Liu et al., 2010). However, deep soil water use (>1 m) has also been reported in tropical rainforests (Nepstad et al., 1994; Fan et al. 2017). These deeper soil water sources contributed considerably more to xylem water overall across our sampled tres than the middle 20–100 cm soil depth. Recent studies on tree water sources in the tropics using the dual isotope approach have shown tree use of >0.2 m soil water (Querejeta et al., 2007; Schwendenmann et al., 2015). But these previous studies used only a few species. Our study of 46 co-occurring species showed that the majority of the observed wet tropical rainforest tree species relied on water from the shallowest soil layer (0.0–0.2 m). Approximately 75% of the contribution to xylem water of the studied trees came from this layer—much higher than all the deeper (0.1–4.0 m) soil layers (Fig. 7). In contrast, some species such as Alloxylon wickhamii, Alangium villosum, Glochidion ferdinandi, Argyrodendron peralatum, Ficus hispida, Pouteria obovoidea, Syzygium claviflorum and Toona ciliata relied mostly on deep soil water. Soil water uptake patterns were therefore



Fig. 6. The $\delta D - \delta^{18} O$ relationship for soil water and xylem water. The local meteoric water line was calculated from rain samples collected during field work.

species-specific, although all species were exposed to the same environmental conditions. It is also interesting to note that all 46 species sourced at least part of their water from deep within the soil profile, though this was only a small proportion for most species.

4.2. Tree functional traits and water uptake depth

It is generally assumed that large trees use more deep soil water than small trees. This is assumed because large-sized trees generally have deeper root systems than small-sized trees (Dawson & Ehleringer, 1991; Horton and Hart, 1998a, 1998b; Romero-Saltos et al., 2005; Goldsmith et al., 2012; Brum et al., 2019). Although some small trees reflected deep soil water use, and some large trees reflected shallow soil water use, isotopic ratio depletion of xylem water was directly proportional to tree size, which is consistent with previous studies showing that large trees generally have deeper roots (e.g. Dawson & Ehleringer, 1991; Goldsmith et al., 2012; Brum et al., 2019). However, our work shows that while tree size had a significant effect on depth contributions from soil water to xylem water, some small trees did tap into deep soil water, while some large trees relied mainly on shallow soil water (Fig. 10). Other studies have also found ambiguous water uptake depths with respect to tree size. Stahl et al. (2013) showed that tree dimensions did not influence water uptake depth in tropical tree species. Furthermore, Thorburn & Ehleringer (1995) as well as Evaristo et al. (2016) found that the roots of a tree in a specific soil layer did not always use water from that layer. For example, Mueller et al. (2005) showed that large trees uptake water from shallow soil layers. Meinzer et al. (1999) showed that smaller tropical trees relied more on deep water than did larger, co-located trees. Past work in Puerto Rico (Evaristo et al., 2016) using mixing models and isotope data showed that during the dry season, large, shallow-rooted Mahogany trees (Swietenia spp.) located on ridge tops relied mostly on deep soil (>20 cm) water, while smaller, deep-rooted Mahogany trees used mostly groundwater.

Some of the trees with low wood density showed a depleted isotope

composition, indicating the use of deep soil water (Fig. 10). Our study showed that, in a highly diverse forest context where the observed species were exposed to similar environmental conditions, depth of water uptake was related to tree size and wood density. Future studies should examine tree root architecture which is likely an important factor in tree water uptake patterns.

4.3. On dual isotopes and the Bayesian approach

Previous studies have shown that using only a single isotope (δ^2 H or δ^{18} O) to assess plant water sources can be problematic since each tracer on its own may provide different information on the potential sources of plant water uptake if samples plot off the meteoric water line (McDonnell, 2014). Interestingly, our dual isotope ratio analysis showed that all the soil water isotope ratios from 0 to 1 m in the plot fell along the LMWL, consistent with the very high humidity and low evaporation rates in this tropical ecosystem. Isotope ratios for the cryogenically extracted soil water from 1 to 4 m depth, sampled outside the plot, however, plotted below the LMWL. When xylem water isotope samples were plotted with the soil samples in the dual isotopic space some xylem samples deviated from the 0-1 m soil water isotope sample cluster, with some plotting along the 1-4 m soil water cluster and some plotting outside both soil mixing spaces, indicating possible fractionation within some species associated with transpiration. Even when plotting outside both soil mixing spaces, most xylem samples still appear to be bound by the LMWL and the soil evaporation line as described by Goldsmith et al. (2012). Possible fractionation effects cannot be incorporated into the traditional mass balance method, however, recent work by Evaristo et al. (2017) showed that the Bayesian mixing model approach which we used in this study is less sensitive to fractionation effects than mass balance methods.

The Bayesian mixing approach was used in this study because of its higher capacity to deal with multiple water sources and mixture ('xylem') compared to the traditional and mass balance method. Early work showed



Fig. 7. The Bayesian mixing model results for source water partitioning per depth interval and per tree species. For easier visualization, means are shown in this figure.

that a mass balance approach might be suitable for two to three sources (e. g., Thorburn & Walker, 1994). However, more recent work has shown that when sources are greater than the number of isotope tracers, the mass balance method cannot adequately deal with this (Moore & Semmens, 2008; Stock & Semmens, 2016). The dataset used in this study included some outliers of xylem water isotopes, indicating possible fractionation effects. The Bayesian approach with multiple sources and mixture ('different xylem water mixture'), provided a range of feasible solutions (Phillips and Gregg, 2003), where prior ecological knowledge can be applied to determine the correct tree water source (Evaristo et al., 2017). We found that 83% of the sampled trees relied mainly on water from a soil depth of 0-0.2 m. This is supported by previous work in tropical rainforest settings showing that trees have most of their root biomass in the upper soil layers to optimize their acquisition of resources such as nutrients (Stahl et al., 2013). In addition, while prior information was not incorporated into the model, root depth observations during soil coring were used to verify that the Bayesian mixing model estimations coincided with the observed rooting depths.

4.4. Our conceptual model: Hydrological niche segregation of plant water use revealed by isotope patterns

Hydrological niche segregation (Fargione et al. 2007; Araya et al 2011, Silvertown et al. 2014) may explain our data patterns because of niche differences among species. Individuals in a polyculture experience less niche overlap for resource use than in comparable monocultures (Yachi and Loreau, 2007; Hooper et al. 2005; Bachmann et al. 2015; Silvertown, 2004; Haggar and Ewel, 1997). Our results show that the soil water displayed simple and predictable patterns in depth and space across the plot (Fig. 5). Soils from each layer of the studied plot were spatially homogenous in terms of soil water isotope composition, and all measures had a predictable pattern with depth. All the plot sampled soil water evaporation in the high humidity tropical forest. As per the individual samples noted above, our interpolated plot level soil water isoscapes also show homogeneity of each soil layer across the plot. But surprisingly and despite spatial homogeneity and predictable linear



Fig. 8. Principle Components Analysis (PCA) of tree traits and xylem water isotope ratios. PC1 indicates that tree size, MBAI and wood density explain the majority of variation in isotope ratios.

Table 2

Results from bivariate Pearson correlations between soil water contribution to xylem (%) and MBAI (n = 40), tree size (DBH) (n = 49) and wood density (n = 49). The *P* value in bold indicates a significant relationship.

Tree trait	0.0–0.2 m		0.2–1.0 m		1.0–2.0 m		2.0–3.0 m		3.0–4.0 m	
	r	р	r	р	r	р	r	р	r	р
Tree size	-0.34	0.01	0.36	0.01	0.35	0.01	0.31	0.02	0.34	0.01
MBAI	-0.30	0.05	0.39	0.01	0.30	0.05	0.27	0.07	0.32	0.03
Wood density	0.28	0.05	-0.27	0.06	-0.28	0.05	-0.27	0.05	-0.27	0.05

changes with depth in soil isotope characteristics, tree xylem data showed striking variability across the plot (Fig. 9). Isotopic ratio depletion of xylem water was directly proportional to tree size. Wood density, tree size and MBAI explained 54.8% of the variation of xylem water isotope ratios (δ^2 H and δ^{18} O) composition in two axes from a principal component analysis (Fig. 8). This indicates tree traits can be used as a useful tool to predict tree water uptake depth patterns. Overall, our results support niche differentiation of the depth in the soil profile from which trees extracted water based on the stable isotopic composition of xylem water. This niche segregation appears largely driven by tree traits such as tree size, wood density and MBAI on the flat, homogeneous plots. Practically speaking, it may be possible that a better understanding of hydrological niche segregation among co-occurring tropical tree species can support improved mixed-species plantation designs and lead to better predictions about future species shifts in response to climate change in tropical forests.

4.5. Uncertainties

In analyzing our results we have assumed that water transport is effectively instantaneous and that the paired soil–water and xylem water samples collected in close temporal proximity to each other reflect this water transport. Evaristo et al (2019) is the only study we are aware of for a physical model of a tropical forest system to examine this assumption directly. That study used an applied tracer approach and found differing transit times from tracer application to the soil surface to the measured tree xylem water sample, which ranged from 17 to 62 days. Recently, De Deurwaerder et al. (2020) showed with a hydraulic

model that sap flow rates could influence the isotopic composition of xylem water, and that there could be diurnal variations larger than the expected error rate. Clearly more work needs to be done in open field conditions to examine this. Still, some of our xylem samples matched the deep (1–4 m) soil water which was sampled approx. 10 days before xylem sampling. We recognize that some of our sampled species may have low-conductivity, high-density wood, and be potentially located in the understory, which may result in low transpiration rates. Such differences in sap flow rates may not be captured by sampling at a single point in time. Further sampling will be needed to address this issue. Nothwithstanding, while we acknowledge that longer term sampling of soil- and xylem water would be an important and useful time series to get at transit times, the snapshot analysis of a remarkably diverse rainforest plot (see Table 1) presented here is a step towards that vision.

In our Bayesian mixing model to assess source contributions to each of the xylem water in 49 trees, we combined soil water extracted through different methods (vapour bag equilibration from 0 to 1 m and cryogenic vacuum extraction from 1 to 4 m) in order to include all possible sources down to 4 m depth. Although cryogenically extracted soil water from 0 to 1 m was excluded from analysis due to risk of evaporation because of the sampling location outside the plot, we used it to test for how using the two methods could have affected the model estimations. This model comparison allowed us to confirm that the approach did not affect our results, and that the contributions estimated for each tree were consistent across all model variations tested. We were able to verify that it was the number of sources used, and not the inclusion or exclusion of the cryogenically extracted soil water, which affected the contribution patterns observed.



Fig. 9. Spatial variation of xylem and soil water across the 0.32 ha plot using the Inverse distance weighting (IDW) interpolation method. The IDW interpolation assumes that points that are close to one another are more alike than the points that are farther apart. To predict a value for any unmeasured location, IDW uses the measured values surrounding the prediction location. Those measured values closest to the prediction location have more influence on the predicted value than those farther away.

Lastly, it is important to consider that the MCMC method used with the Bayesian mixing models in MixSIAR estimates probability distributions for the proportion of each source contributing to the mixture, which can be then summarized into medians and credible intervals (Stock and Semmens, 2016). While the median is a summary estimate, the credible intervals provide a measure of the uncertainty of the estimated proportion, or the "range of feasible solutions" (Phillips and Gregg, 2003). In our case, the greatest source of water overall across our sampled trees was the shallow 0-20 cm soil. However, it is important to clarify that these are *probable* proportions and not *absolute* proportions. There is some uncertainty associated to the 100-200 cm and 300-400 cm depths (see supplementary Fig. 4). This can be attributed to the higher negative correlation between the posterior distributions of these sources shown in the matrix plot, which implies that for estimated proportions of these two sources, for one to increase the other must decrease. Considering this, we can more generally interpret that soil deeper than 100 cm is probably the second most important water source for our sampled trees overall, but we cannot absolutely conclude that the proportion estimated for the 100-200 cm depth (9.8%) is greater than the 300-400 cm depth (5.6%).

5. Conclusion

We performed a Bayesian mixing analysis of tree water isotope patterns to better understand the water uptake depth patterns of 46 colocated tropical rainforest tree species. Our results indicated that there was variation in soil water uptake depth among the observed species because of tree size, wood density and growth rate, suggesting tree traitspecific behaviours. The dual isotope analysis together with the Bayesian mixing model for individual trees showed that the shallow soil water pool (0–0.2 m) was the source of the majority of water transpired by these tropical rainforest tree species. This finding is consistent with the general assumption that tropical rainforest trees have most of their root biomass in the upper soil layers to optimize their acquisition of nutrients and water. The study provides an example of how a dual isotope approach can be applied to better understand the water uptake strategies of tropical forest tree species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.



Fig. 10. Influence of tree traits on spatial patterns of isotopic composition (δD and $\delta^{18}O$) of xylem water. Tree functional traits were overlaid on the interpolated xylem isotope layer. Growth form 'F', 'VF', 'M' and 'S' indicate fast, very fast, moderate and slow growing species, respectively. Successional status 'P' 'ES', 'LS' and 'M' indicate pioneer, early successional, late successional and mature phase species. For MBAI (mean basal area increment), wood density and tree size, circle size represents value, with small circles indicating lower value and bigger circles higher value.

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Author contributions

Md. Shawkat I. Sohel: Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Methodology, Writing - original draft, Writing - review & editing, Funding acquisition. Adriana Vega Grau: Formal analysis, Visualization, Writing - review & editing. Jeffrey J. McDonnell: Conceptualization, Investigation, Methodology, Data curation, Writing - review & editing, Supervision. John Herbohn: Conceptualization, Investigation, Methodology, Data curation, Writing review & editing, Funding acquisition, Resources, Supervision.

Appendix A. Supplementary material

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