



Functional Groups Mask Inter- and Intraspecific Variation in Water Use Strategies in a Seasonally Dry Tropical Forest

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Across the karst landscape of Quintana Roo, Mexico, plant access to nutrients and water appears limited by generally shallow soil. However, underlying this surface are heterogenous pockets in bedrock and deeper, stable groundwater, suggesting the potential for specialization by species in accessing soil resources. If species differentially access rock resources, divisions by functional groups may also be expected. In this study, shallow caves provided an opportunity to assess resource use strategies by direct, species-specific root observations coupled with traditional above ground measurements. Utilizing stable isotopes from stems and leaves ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$), we investigated water access and water use efficiency of trees during the dry season to uncover relationships between rooting habit, tree size, and pre-determined functional groups based on leaf habit and wood density. Functional group membership did not predict measured stable isotope ratios, indicating that functional groups were poor predictors of resource use. We did find evidence for deep water use by select species and larger individuals. Interestingly, as trees became larger, $\delta^{13}\text{C}$ increased to a threshold but then declined, suggesting increasing vulnerability to water limitation as trees increase in size, consistent with other seasonally dry tropical forests. Our work demonstrates that, although shallow soils likely drive strong resource limitations, co-occurring trees in karst ecosystems employ diverse resource acquisition strategies, suggesting important consequences for community composition and ecosystem function in the face of environmental change.

Keywords: seasonally dry tropical forest, water use strategies, functional groups, stable isotopes, ecophysiology

INTRODUCTION

In seasonally dry habitats, plants often face a fundamental tradeoff between maintaining functional water status and sufficient C uptake (McDowell et al., 2008). Several plant traits have been identified as adaptive in these environments. These include high stomatal sensitivity (Henry et al., 2019), low leaf mass per area (Givnish, 2002; Wright et al., 2004), high cavitation resistance (Steddele, 2001; Sperry, 2003; Chave et al., 2009; Trueba et al., 2017), deciduousness (Álvarez-Yépiz et al., 2017), and deep roots for better access to reliable water (Doody and Benyon, 2011; Nardini et al., 2016; Pierret et al., 2016). Given high species diversity, particularly in tropical habitats, classification strategies, like resource conservative vs. acquisitive have been derived primarily from leaf traits (Aerts, 1995; Reich, 2014). Researchers have further attempted to link leaf traits with root traits to establish

whole plant functional groups (Freschet et al., 2015; McCormack et al., 2015). However, several studies have demonstrated apparent disconnects between the above and below ground function and a coherent whole plant approach remains elusive (Roumet et al., 2016; Weemstra et al., 2016; Kleinschmidt et al., 2020). Thus, a gap in our understanding of how root traits interact with better characterized leaf and wood traits persists (Grew, 1692; Yamauchi et al., 2021; Zhou et al., 2022).

Seasonally dry tropical forests are compelling ecosystems to investigate resource use strategies due to apparently obvious challenges associated with water availability (Santiago et al., 2004). Several studies report niche separation based on functional groups (Kitajima and Poorter, 2008; Markesteijn et al., 2011; Álvarez-Yépiz et al., 2017), with evergreens having advantages over deciduous species due to conservative strategies expected to be associated with longer leaf lifespans and persistence of carbon gain into dry periods (Mitchell et al., 2008; Hasselquist et al., 2010; Ellsworth and Sternberg, 2015). Wood density is also associated with water use strategies, following observations of species with low wood density and high hydraulic efficiency employing a “boom-and-bust” style while species with high wood density tend to align with conservative traits (Méndez-Alonzo et al., 2012; Reich, 2014). Contrarily, others have noted that functional groups were not useful in predicting differences in water-use strategies in dry tropical forests (Powers and Tiffin, 2010; Werden et al., 2018). Significant intra- and interspecific variation among traits and resource use strategies observed in seasonally dry tropical forests add complexity to functional group organizational schemes, potentially weakening their utility in these systems (Hulshof and Swenson, 2010; Xu et al., 2016; Santiago et al., 2017; Derroire et al., 2018). However, continued research to understand resource acquisition strategies and underlying drivers is crucial for conservation efforts and predictions for plant responses to climate change. In addition, seasonally dry tropical forests are among the most threatened of global tropical forests, often impacted by deforestation for agriculture and urbanization (Arturo Sánchez-Azofeifa et al., 2005), despite the fact that they are crucial landscapes for carbon sequestration and storage (Becknell et al., 2012) and home to notably high phylogenetic and functional diversity (Eamus, 1999; Cavender-Bares et al., 2016; DRYFLOR, 2016).

We studied a seasonally dry tropical forest in the eastern Yucatán Peninsula, which provided an ideal setting to assess relationships between water use efficiency, plant function, and apparent rooting strategies. Semi-evergreen tropical forests dominate in the eastern state of Quintana Roo (Ibarra-Manríquez et al., 2002; Durán-García et al., 2016) where there is a dry season from November to May, in which 20% of the annual precipitation falls. The peninsula is a vast karst landscape, which is expected to exacerbate this limitation by limiting surface or soil water availability (Geekiyana et al., 2019). The region is generally characterized by roughly 10 centimeter deep soils atop limestone bedrock where water content and storage vary with the heterogeneous distribution of cavities in the rock (Querejeta et al., 2007; Estrada-Medina et al., 2013a; Fragoso-Servón et al., 2020). This surface dynamism is contrasted by the karst aquifer, a

reliable water source, that underlies the entire peninsula (Bauer-Gottwein et al., 2011). In our study area, the distance to the surface of the freshwater lens varies from 4 to 5 m deep, but may be between 9 and 20 meters deep near Mérida in the northwest (Hasselquist et al., 2010; Estrada-Medina et al., 2013a; Durán-García et al., 2016). The increase in abundance of evergreen species as precipitation increases and depth to groundwater decreases from west to east prompts questions about functional group dependence on groundwater and how this relates to other plant traits (Nepstad et al., 1994; Bleby et al., 2010; Swaffer et al., 2014; Nardini et al., 2016).

Below ground, extensive cave systems have formed by dissolution of the limestone bedrock (Smart et al., 2006; van Hengstum et al., 2010). In these caves, it is common to see tree roots emerging from conduits in the ceiling, walls, and speleothems (Adams et al., 2020b). Observations of roots in contact with groundwater in many areas of the eastern peninsula provide evidence that some trees are indeed accessing and utilizing deep water. Although commonly observed in these caves, very little is known about the role deep water access plays in water stress tolerance for these species and how rooting habits relate to other characteristics of these trees.

We report here a field-based effort to characterize relationships between access to groundwater and inferred water stress and whether these were consistent with expectations from functional group theory. We made three specific predictions: (1) evergreen species would have relatively high water use efficiency, but be more reliant on groundwater than deciduous species, with more abundant roots in caves than deciduous species, (2) trees with lower wood density (irrespective of leaf habit) would have lower water use efficiency and be more reliant on deep water with abundant roots in caves than high wood density species, and (3) species with larger individuals aboveground would also be dominant in the caves with consistent deep-water access.

MATERIALS AND METHODS

Site Description and Plot Establishment

Our field sites were in the eastern state of Quintana Roo, Mexico. This portion of the Yucatán peninsula receives between 1200 to 1500 mm of precipitation annually, with a dry period from November to May (Bauer-Gottwein et al., 2011; Durán-García et al., 2016). Forests are classified as semi-evergreen, with approximately 25% of the trees losing leaves in the dry season (Sánchez-Sánchez and Islebe, 2002). This work was conducted at four sites along the Caribbean coast of Quintana Roo. The sites, Cueva Culebron, Jaguar Maw, Nohoch Aktun, and Ruta de los Guerreros, were located between the cities of Paamul and Akumal. Each site was associated with a cave network, allowing direct access to roots and groundwater. Because an important aim was to directly connect the surface trees to their subterranean roots, detailed cave maps were required for each (Trimmis, 2018). Using cave survey data, surface plots (100 m²) were randomly established at each site directly above cave passages and paired with below ground plots used to assess root biodiversity and abundance (Adams, 2020). Using survey data, GPS locations on the surface mirroring the location of georeferenced survey

stations below ground were gathered before arriving at the sites (see the **Supplementary Materials** for details). Two plots were randomly selected from these candidates at each site.

Vegetation Surveys

Field work was conducted between December 28, 2017 and January 8, 2018, during the dry season to capture differences in water use strategies during a time of limited water availability. To assess above ground community composition, all individuals were identified to species either in the field or *via* subsequent DNA barcoding (Adams, 2020). All trees with a diameter at breast height (DBH) ≥ 5 cm were recorded. Basal area was calculated for each tree and compiled by species and site. Using the cave at each site, we collected root samples in the paired below ground plots and later identified species reaching into the caves to groundwater with DNA barcoding (Adams, 2020). Based on these observations, species were organized into three rooting habit groups: above ground only (roots never observed in caves), rare below ground (<5% relative abundance), and common below ground (>5% relative abundance). For a full summary of the above and below ground community composition, (see **Supplementary Table 1**).

Stems and leaves of all individuals measured were collected for stem water ($\delta^{18}\text{O}$ and $\delta^2\text{H}$) and leaf C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) stable isotope analysis. Stems were stripped of bark in the field and quickly placed in glass scintillation vials with lined screw caps (12 mL, Wheaton-DWK Life Sciences, Millville, NJ, USA). Caps were wrapped with Parafilm to prevent loosening. Vials were stored on ice in the field and then frozen until transport to the United States. Leaves for C and N isotope analysis were placed in Whirlpak bags (Nasco, Fort Atkinson, WI, USA) filled with silica gel (VWR International, LLC, Radnor, PA, USA) to rapidly dry the leaves. Silica gel included indicator and was replaced as necessary in the bags as the leaves dried.

Soil samples were collected in the middle of the north half of each plot. These samples were later used to characterize the isotopic composition of soil water. Soil was collected at 5 and 10 cm from the surface after removing the litter layer. Scintillation vials were filled three quarters full, sealed, stored, and transported as above for stems. When samples arrived at Texas A&M University, stem and soil samples were stored in a freezer (0°C) for later processing. Leaves were stored in the lab with added silica gel to ensure samples remained dry until processing.

Water was also sampled from pools in the caves for a synoptic assessment of groundwater isotope ratios. For collection, glass vials (20 mL, VWR International, LLC, Radnor, PA, USA) were filled completely to minimize headspace and capped and sealed as above. Once at Texas A&M University, water samples were stored in a refrigerator (4°C) until stable isotope analysis.

Categorizing Functional Groups

Tree species were organized into functional groups based on leaf habit and wood density. Associated information was gathered from existing literature from the Yucatán Peninsula and other tropical forests (**Supplementary Table 1**). Distinction between lightwoods, softwoods, and hardwoods followed Borchert (1994),

with wood density values of <0.05, 0.5–0.8, and >0.8 g cm⁻³, respectively.

Sample Processing

Water was extracted from stem and soil samples *via* cryogenic vacuum distillation. Extractions were performed at 100°C on a closed vacuum extraction line (West et al., 2006). We recognize that extraction temperature and other variables like soil texture and mineralogy potentially interact to affect the isotopic composition of extracted water (Adams et al., 2020a). We chose to perform extractions at this temperature to be consistent with other published work and with our objective of comparing among individuals with access to soils with similar clay content (Orlowski et al., 2016). Extractions were considered complete when no further visible condensation was observed in the cold finger. Two stem samples were outliers with evaporative losses from the extraction process and were removed from subsequent analyses.

Water samples were transferred into vials (0.3 mL, Wheaton-DWK Life Sciences, Millville, NJ, USA) for stable isotope analysis. Analyses were performed using a Delta V Advantage isotope ratio mass spectrometer (IRMS) linked to a High Temperature Conversion/Elemental Analyzer (TC/EA) *via* a ConFlo IV (Thermo Fisher Scientific, Waltham, MA, USA). Calibration standards were: SIBS-wA ($\delta^{18}\text{O} = -50.10\text{‰}$, $\delta^2\text{H} = -390.8\text{‰}$), SIBS-wP ($\delta^{18}\text{O} = -4.61\text{‰}$, $\delta^2\text{H} = -34.1\text{‰}$) and a QC check with SIBS-wU ($\delta^{18}\text{O} = -15.97\text{‰}$, $\delta^2\text{H} = -120.2\text{‰}$).

Leaves for C and N isotope analysis were ground to powder using a Ball Mill (MM 400; Retsch GmbH, Haan, Germany), placed in tin capsules, and weighed prior to isotope analysis (EA-IRMS; Costech Analytical Technologies Inc., Valencia, CA, USA). Calibration standards were: USGS 40, $\delta^{13}\text{C} = -26.39\text{‰}$, $\delta^{15}\text{N} = -4.52\text{‰}$ and USGS 41, $\delta^{13}\text{C} = 36.55\text{‰}$, $\delta^{15}\text{N} = 47.55\text{‰}$. All sample processing and stable isotope analysis was performed at the Stable Isotopes for Biosphere Science (SIBS) Laboratory (<https://sibs.tamu.edu>) at Texas A&M University.

Leaves from 6 individuals that spanned the range of found tree size were analyzed for $\Delta^{14}\text{C}$ to determine if root-derived bicarbonate could be a source of CO₂ for leaf photosynthesis, potentially increasing with tree size (Berry, 1989; Hang and Wu, 2016; Rao and Wu, 2017). Analyses were conducted at the W.M. Keck-Carbon Cycle Accelerator Mass Spectrometry (KCCAMS) facility at University of California-Irvine (<https://sites.uci.edu/keckams/>). Radiocarbon concentrations were given as fractionation-corrected fraction modern ($F^{14}\text{C}$), $\Delta^{14}\text{C}$, and conventional radiocarbon age, following Stuiver and Polach (1977). All samples were classified as “modern”. We found no relationship between $F^{14}\text{C}$ and $\delta^{13}\text{C}$ ($R^2 = -0.25$, $p = 0.96$), allowing us to interpret $\delta^{13}\text{C}$ solely as a function of leaf physiology (**Supplementary Table 3**).

Stable Isotope Analysis

Isotopic composition of stem water from individual trees was compared to soil water and cave water collected from each site. This allowed for evaluation of an individual tree’s water

source, given the assumption that stem water is a weighted average of the water acquired by the tree and there is no fractionation during water uptake (Ehleringer and Dawson, 1992). Trees were identified as utilizing shallow water if it resembled the heavy isotope-enriched soil water value or deep water if it resembled the heavy isotope-depleted cave water value. We did not attempt to quantify a quantitative fraction of groundwater use, as we were interested in relative differences among individuals.

Statistical Evaluation

Data analysis was carried out with the statistical software R (R Core Team, 2019) run in RStudio (RStudio Team, 2019). Model residuals were checked for normality using the Shapiro-Wilk normality test and checked for equal variance with the Brown-Forsythe test. The $\delta^2\text{H}$ residuals were not normal and were transformed before analysis. Effect of site, species, rooting habit, basal area, and functional group on $\delta^{18}\text{O}$, $\delta^2\text{H}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ values were evaluated using one-way ANOVAs. Welch's tests were used when residuals violated ANOVA assumptions. A summary of these analyses can be found in **Supplementary Table 4**. TukeyHSD mean comparisons and Games-Howell *post hoc* tests provided insight into the differences between groups. Linear regressions were used to assess the overall relationship between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$. Separate linear regressions were performed for each rooting habit group to isolate potential patterns in water use and efficiency among these individuals. Similarly, linear regressions were used to assess the overall relationship between $\delta^{18}\text{O}$ and $\delta^{15}\text{N}$ as well as separate analyses for non-legumes and legumes. This analysis was performed to determine if patterns in nitrogen availability in tropical karst systems complimented rooting depth and water use observations. A summary of these analyses can be found in **Supplementary Table 5**. Independent, two sample *t*-tests were employed to determine if there were differences in soil water isotopes from different depths and cave water collected from different seasons.

RESULTS

Water Stable Isotopes

Cave water was collected during the dry season from Cueva Culebron and Ruta de los Guerreros and during the wet season (August 2017) at Ruta de los Guerreros and Nohoch Aktun. No cave water samples were collected at Jaguar Maw as there was no exposed water in this system. Independent, two sample *t*-tests showed that water collected in the dry season did not differ from water collected during the wet season for both $\delta^{18}\text{O}$ and $\delta^2\text{H}$ ($t_{14} = 1.89$, $p = 0.08$ and $t_{14} = -0.15$, $p = 0.88$, respectively). The average isotopic composition of cave water was $\delta^{18}\text{O}$: $-4.48 \pm 0.25\text{‰}$; $n = 11$, $\delta^2\text{H}$: $-27.1 \pm 1.6\text{‰}$. Soil water from 5 and 10 cm in the dry season was $\delta^{18}\text{O}$: $-1.4 \pm 0.69\text{‰}$; $n = 12$, $\delta^2\text{H}$: $-14.1 \pm 4.2\text{‰}$. There was not a significant difference between depths for either $\delta^{18}\text{O}$ or $\delta^2\text{H}$ ($t_{10} = -1.24$, $p = 0.24$ and $t_{10} = -1.05$, $p = 0.32$, respectively).

Stem water $\delta^{18}\text{O}$ values across all samples ranged from -4.93 to -1.57‰ , with an average of $-3.21 \pm 0.79\text{‰}$. $\delta^2\text{H}$ values

ranged from -37.7 to -11.5‰ with an average of $-22.8 \pm 6.1\text{‰}$. $\delta^{18}\text{O}$ varied significantly across sites ($F_{3, 67.5} = 6.81$, $p < 0.01$). Trees from Cueva Culebron had stem water that was heavy isotope-depleted compared to Jaguar Maw ($t_{64.9} = 4.43$, $p < 0.01$; **Table 1**). $\delta^2\text{H}$ values from stem water also significantly varied by site ($F_{3, 70.7} = 16.3$, $p < 0.01$), with all sites being different from each other, except Nohoch Aktun overlapped with Ruta de los Guerreros ($t_{52.7} = 0.33$, $p = 0.99$; **Table 1**). Jaguar Maw was had the highest mean $\delta^2\text{H}$, matching the pattern observed for $\delta^{18}\text{O}$.

Leaf Stable Isotopes

Across sites, leaf $\delta^{13}\text{C}$ ranged from -35.3 to -27.4‰ , with an average of $-31.1 \pm 1.5\text{‰}$. There was a significant difference in $\delta^{13}\text{C}$ values among sites ($F_{3, 68.6} = 2.90$, $p = 0.04$), with the difference between Ruta de los Guerreros and Jaguar Maw appearing to drive this site effect ($t_{74.6} = 2.62$, $p = 0.05$; **Table 1**).

Leaf $\delta^{15}\text{N}$ varied from -1.9 to 4.8‰ , with an average of $1.2 \pm 1.2\text{‰}$. As expected, legumes had $\delta^{15}\text{N}$ values that were closer to 0‰ , compared to non-nitrogen fixing species ($F_{1, 142} = 17.1$, $p < 0.01$). $\delta^{15}\text{N}$ increased with increasing $\delta^{18}\text{O}$ values among individual trees ($R^2 = 0.11$, $p < 0.01$), with legumes and non-legumes both having significantly positive relationships ($R^2 = 0.26$, $p = 0.01$ and $R^2 = 0.07$, $p < 0.01$, respectively; **Figure 1A**). There was a significant difference in $\delta^{15}\text{N}$ values by site ($F_{3, 68.9} = 23.8$, $p < 0.01$), with sites being different from each other except for Cueva Culebron and Jaguar Maw ($t_{73.3} = 1.71$, $p = 0.32$; **Table 1**). Nohoch Aktun had the highest $\delta^{15}\text{N}$ values and was associated with dominance by *O. lanceolata*, a shallow rooted species. Ruta de los Guerreros had the lowest $\delta^{15}\text{N}$ values, consistent with *S. cubensis*, a legume, being the most common tree at this site.

Water and Carbon Isotopes Based on Rooting Habit

Three genera/species were identified as common below ground, all evergreens: *Ficus* spp. *Pouteria* spp. and *Leucaena leucocephala* (Lam.) de Wit (*Ficus* and *Pouteria* could not be identified lower than genus level). Of the 29 tree species with roots exposed in the caves, 17 were evergreen and 12 were deciduous. The rare below ground group was fairly equally represented by evergreen (47%) and deciduous (53%) species. Overall, 49% of evergreens observed above ground had roots in caves compared to 63% of deciduous species.

$\delta^{18}\text{O}$ and $\delta^2\text{H}$ from extracted stem water did not differ between rooting habit groups ($F_{2, 139} = 0.19$, $p = 0.83$ and $F_{2, 139} = 2.71$, $p = 0.07$, respectively; **Table 2**). Likewise, leaf $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ did not differ between rooting habit groups ($F_{2, 140} = 0.75$, $p = 0.47$ and $F_{2, 141} = 0.75$, $p = 0.48$, respectively; **Table 2**). The relationship with $\delta^{15}\text{N}$ did not change when legumes were excluded from the analysis ($F_{2, 118} = 1.89$, $p = 0.16$).

We observed a negative correlation across all individuals between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ ($R^2 = 0.10$, $p < 0.01$; **Figure 1B**). Separating individuals into their respective rooting habit groups based on root abundance revealed differences in the relationship between C and O isotopes (**Figure 2**). Individuals in the rare below ground and common below ground groups both have

TABLE 1 | Mean and standard deviation (1σ) of $\delta^{18}\text{O}$, $\delta^2\text{H}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ at each study sites.

Site	Number of stems/leaves	$\delta^{18}\text{O}$	$\delta^2\text{H}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Cueva Culebron	43/43	$-3.59 \pm 0.93_a$	$-26.7 \pm 6.5_a$	$-31.2 \pm 1.6_{ab}$	$1.1 \pm 1.1_a$
Ruta de los Guerreros	43/44	$-3.19 \pm 0.72_{ab}$	$-22.3 \pm 5.3_b$	$-30.7 \pm 1.5_a$	$0.4 \pm 1.0_b$
Nohoch Aktun	23/23	$-3.07 \pm 0.76_{ab}$	$-22.7 \pm 4.4_{ab}$	$-30.7 \pm 1.5_{ab}$	$2.5 \pm 1.0_c$
Jaguar Maw	33/34	$-2.86 \pm 0.47_b$	$-18.3 \pm 4.1_c$	$-31.5 \pm 1.2_b$	$1.5 \pm 1.0_a$
Analysis					
Test statistic		$F_{3, 67.5} = 6.81$	$F_{3, 70.7} = 16.3$	$F_{3, 68.6} = 2.90$	$F_{3, 68.9} = 23.8$
P-value		<0.01	<0.01	0.04	<0.01

Legumes are included in the $\delta^{15}\text{N}$ analysis. $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values were obtained from stem water while $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were obtained from leaves. Numbers within the same column that do not share the same subscript differ at $p < 0.05$.

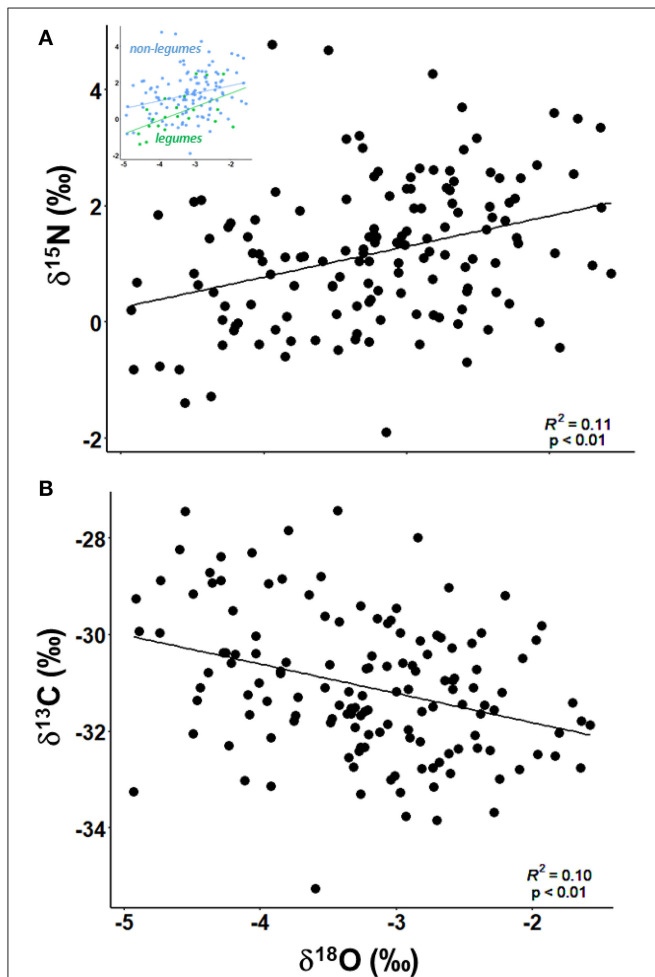


FIGURE 1 | Relationships between $\delta^{18}\text{O}$ from stem water and $\delta^{15}\text{N}$ [(A); $R^2 = 0.11$, $p < 0.01$] and $\delta^{13}\text{C}$ [(B); $R^2 = 0.10$, $p < 0.01$] from leaves among individual trees. The inset in (A) depicts the linear regressions for non-legumes ($R^2 = 0.07$, $p < 0.01$) and legumes ($R^2 = 0.26$, $p = 0.01$).

significant relationships between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values ($R^2 = 0.09$, $p < 0.01$ and $R^2 = 0.55$, $p < 0.01$, respectively), while individuals in the above group only group do not ($R^2 = 0.02$, $p = 0.13$).

Water Use Strategies Among Functional Groups

There was no statistical effect of leaf habit (evergreen vs. deciduous) for $\delta^{18}\text{O}$, $\delta^2\text{H}$, or $\delta^{13}\text{C}$ ($F_{1, 140} = 1.05$, $p = 0.31$, $F_{1, 140} = 0.03$, $p = 0.87$, and $F_{1, 141} = 2.4$, $p = 0.12$, respectively). Leaf $\delta^{15}\text{N}$ among evergreens was significantly more heavy-isotope enriched compared to deciduous species when evaluated with and without legumes ($F_{1, 142} = 8.87$, $p < 0.01$ and $F_{1, 119} = 6.89$, $p < 0.01$, respectively).

Stem water and leaf C isotopes did not differ among wood density groups ($F_{2, 132} = 1.32$, $p = 0.27$, $F_{2, 132} = 2.61$, $p = 0.08$, and $F_{2, 133} = 0.37$, $p = 0.69$, respectively). Leaf $\delta^{15}\text{N}$ did not differ by wood density group when analyzed with legumes ($F_{2, 134} = 0.45$, $p = 0.64$), but when legumes were excluded, wood density groups differed ($F_{2, 111} = 3.94$, $p = 0.02$). In this case, hardwoods were significantly ^{15}N -enriched compared to softwoods ($p = 0.02$).

Functional groups based on leaf habit and wood density together did not yield significant differences in $\delta^{18}\text{O}$, $\delta^2\text{H}$, or $\delta^{13}\text{C}$ values ($F_{5, 129} = 0.92$, $p = 0.47$, $F_{5, 129} = 1.31$, $p = 0.27$, and $F_{5, 130} = 1.33$, $p = 0.26$, respectively; Table 3). Leaf $\delta^{15}\text{N}$ differed by functional group for the complete dataset ($F_{5, 25.8} = 2.64$, $p = 0.05$; Table 3) and when legumes were removed ($F_{4, 109} = 2.65$, $p = 0.04$), with evergreen hardwoods being heavy-isotope enriched compared to deciduous softwoods ($p = 0.03$).

Water and Carbon Isotopes Based on Tree Size

$\delta^{18}\text{O}$ values from extracted stem water were significantly different among size classes ($F_{5, 136} = 3.35$, $p < 0.01$); Figure 3A). The two largest size classes based on DBH (25 to 29.9 cm and 30 to 34.9 cm) had a relatively narrow range of heavy isotope-depleted values, while the other four size classes (5 to 9.9 cm, 10 to 14.9 cm, 15 to 19.9 cm, and 20 to 24.9 cm) had a wide range of $\delta^{18}\text{O}$, with relatively heavy isotope-enriched means for each group. However, $\delta^2\text{H}$ did not vary with DBH ($F_{5, 136} = 2.10$, $p = 0.07$; Supplementary Table 6).

With regards to leaf $\delta^{13}\text{C}$, as DBH increased, $\delta^{13}\text{C}$ values became increasingly heavy isotope-enriched yet became heavy isotope-depleted after trees reached a certain size, seemingly around 20 cm in diameter ($F_{5, 137} = 5.70$, $p < 0.01$; Figure 3B). Leaf $\delta^{15}\text{N}$, evaluated with and without legumes, varied with

TABLE 2 | Mean and standard deviation (1σ) of stem water $\delta^{18}\text{O}$ and $\delta^2\text{H}$ as well as leaf $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ by rooting habit groups.

Rooting habit	Number of stems/leaves	$\delta^{18}\text{O}$	$\delta^2\text{H}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$ (with legumes)	Number of non-legumes	$\delta^{15}\text{N}$ (without legumes)
Above ground only	55/57	-3.23 ± 0.82	-23.9 ± 5.6	-31.2 ± 1.6	1.1 ± 1.2	44	1.4 ± 1.1
Rare below ground	67/67	-3.17 ± 0.72	-21.7 ± 6.3	-30.9 ± 1.3	1.3 ± 1.3	59	1.4 ± 1.2
Common below ground	20/20	-3.29 ± 0.94	-23.5 ± 6.5	-31.2 ± 1.4	1.0 ± 1.3	18	0.9 ± 1.4
Analysis							
Test statistic		$F_{2, 139} = 0.19$	$F_{2, 139} = 2.71$	$F_{2, 140} = 0.75$	$F_{2, 141} = 0.75$		$F_{2, 118} = 1.89$
P-value		0.83	0.07	0.47	0.48		0.16

Species classified as common below ground had relative root abundance of 5% or greater. There were no statistical differences between groups and stable isotope values from stems and leaves.

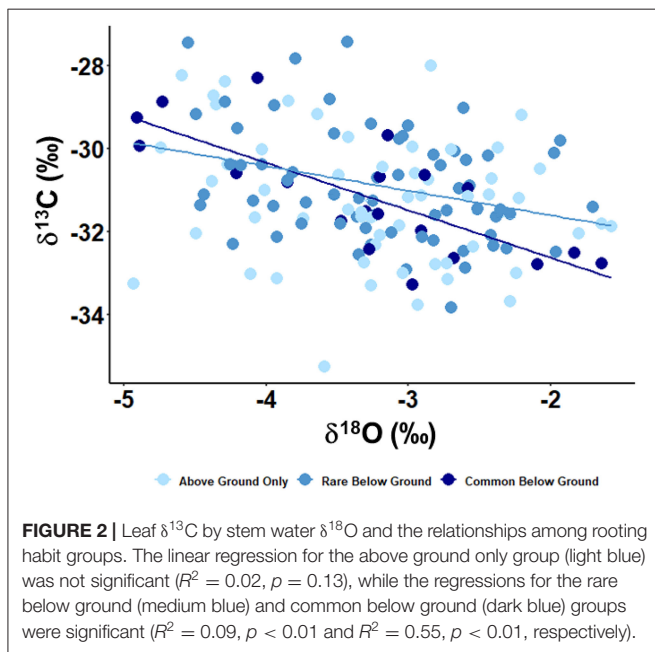


FIGURE 2 | Leaf $\delta^{13}\text{C}$ by stem water $\delta^{18}\text{O}$ and the relationships among rooting habit groups. The linear regression for the above ground only group (light blue) was not significant ($R^2 = 0.02$, $p = 0.13$), while the regressions for the rare below ground (medium blue) and common below ground (dark blue) groups were significant ($R^2 = 0.09$, $p < 0.01$ and $R^2 = 0.55$, $p < 0.01$, respectively).

DBH ($F_{5, 138} = 2.61$, $p = 0.03$ and $F_{5, 115} = 2.90$, $p = 0.02$, respectively; **Figure 3C**). $\delta^{15}\text{N}$ had a similar, though inverted, non-linear pattern as $\delta^{13}\text{C}$.

Species-Level Differences

Species-level effects were significant for all isotope ratios measured ($\delta^{18}\text{O}$: $F_{44, 97} = 1.57$, $p = 0.03$; $\delta^2\text{H}$: $F_{44, 97} = 1.99$, $p < 0.01$; $\delta^{13}\text{C}$: $F_{44, 98} = 3.68$, $p < 0.01$; $\delta^{15}\text{N}$: $F_{44, 97} = 6.54$, $p < 0.01$). Focusing specifically on $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$, we evaluated species differences in water use and water use efficiency (**Figure 4**). Despite differing root habit and functional groups, species with shallow water access (less negative $\delta^{18}\text{O}$ values) and deep water access (more negative $\delta^{18}\text{O}$ values) in general had overlapping $\delta^{13}\text{C}$ [e.g., *D. lateriflora*, *Cordia gerascanthus* L., and *Pouteria reticulata* (Engl.) Eyma]. Variation within species appeared to be attributed to size. For example, *N. psychotrioides*, *V. gaumeri* and *F. obtusifolia* individuals ranged in DBH from 7.3 to 13.1 cm, 7.4 to 14.4 cm, and 8.8 to 19.2 cm, respectively. All three species showed a comparably

wide range of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$. While some species express expected patterns in water use and water use efficiency based on leaf habit, wood density, rooting habit, tree size, and life history (e.g., *M. zapota* was represented in the largest DBH size class, had roots present in caves, had low $\delta^{18}\text{O}$ stem water and relatively low $\delta^{13}\text{C}$), many do not follow expected patterns (e.g., although *S. cubensis* is an evergreen species observed above ground only, individuals had low mean $\delta^{18}\text{O}$ and relatively high $\delta^{13}\text{C}$).

DISCUSSION

The results of our study showed that water utilization and water use efficiency among co-occurring species in Quintana Roo was generally not predicted by rooting habit or functional groups based on leaf habit or wood density, implying that generalizations about rooting depth and resource use strategies based on functional groups may be difficult in this system. Tree size was important, with larger trees in general utilizing deeper water sources than smaller trees. However, deep water use did not correlate with lower water use efficiency. Interestingly, smaller trees and those with shallow water access generally expressed the lowest water use efficiency, contrary to our expectation that these trees would face the greatest water limitation. Our assessment of multiple species allowed us to capture the inter- and intra-specific variation in water access in this karst landscape.

Evergreen and Deciduous Species Have Overlapping Root Zones

Through direct access to roots in caves, we tested expectations about rooting depth and deep water access based on leaf habit (evergreen vs. deciduous). We identified 29 tree species in the caves, consistent with our expectation that many species have access to groundwater *via* deep roots in this seasonally dry, shallow soil ecosystem (Adams, 2020). Yet, there was tremendous variation among species in this access. Three evergreen species: *Ficus* spp., *Pouteria* spp., and *L. leucocephala* were the most common below ground. While this is consistent with our prediction that evergreens would be most common below ground, a large majority (15 of 22) evergreen species observed above ground were never observed in the caves

TABLE 3 | Mean and standard deviation (1σ) of $\delta^{18}\text{O}$, $\delta^2\text{H}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ by functional group based on leaf habit and wood density.

Leaf Habit	Wood density	Number of stems/leaves	$\delta^{18}\text{O}$	$\delta^2\text{H}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$ (with legumes)	Number of non-legumes	$\delta^{15}\text{N}$ (without legumes)
Deciduous	Lightwood	5/5	-3.59 ± 0.92	-25.0 ± 8.2	-31.5 ± 3.0	0.8 ± 0.4	5	$0.8 \pm 0.4^{\text{ab}}$
	Softwood	26/26	-3.23 ± 0.81	-22.2 ± 7.1	-30.6 ± 1.5	0.7 ± 1.2	22	$0.9 \pm 1.0^{\text{a}}$
	Hardwood	5/5	-3.58 ± 0.45	-26.7 ± 4.3	-30.5 ± 0.9	0.4 ± 0.7	0	N/A
Evergreen	Lightwood	26/26	-3.27 ± 0.86	-22.6 ± 6.8	-30.9 ± 1.4	1.4 ± 1.7	26	$1.4 \pm 1.7_{\text{ab}}$
	Softwood	38/38	-3.04 ± 0.79	-22.0 ± 5.7	-31.4 ± 1.3	1.3 ± 0.9	35	$1.2 \pm 0.9_{\text{ab}}$
	Hardwood	35/37	-3.32 ± 0.79	-24.2 ± 5.0	-30.9 ± 1.3	1.3 ± 1.2	26	$1.9 \pm 0.9_{\text{b}}$
Analysis								
Test statistic			$F_{5,129} = 0.92$	$F_{5,129} = 1.31$	$F_{5,130} = 1.33$	$F_{5,25.8} = 2.64$		$F_{4,109} = 2.65$
P-value			0.47	0.27	0.26	0.05		0.04

$\delta^{18}\text{O}$ and $\delta^2\text{H}$ values were obtained from stem water while $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were obtained from leaves. For $\delta^{15}\text{N}$ values (without legumes), numbers within the same column that do not share the same subscript differ at $p < 0.05$.

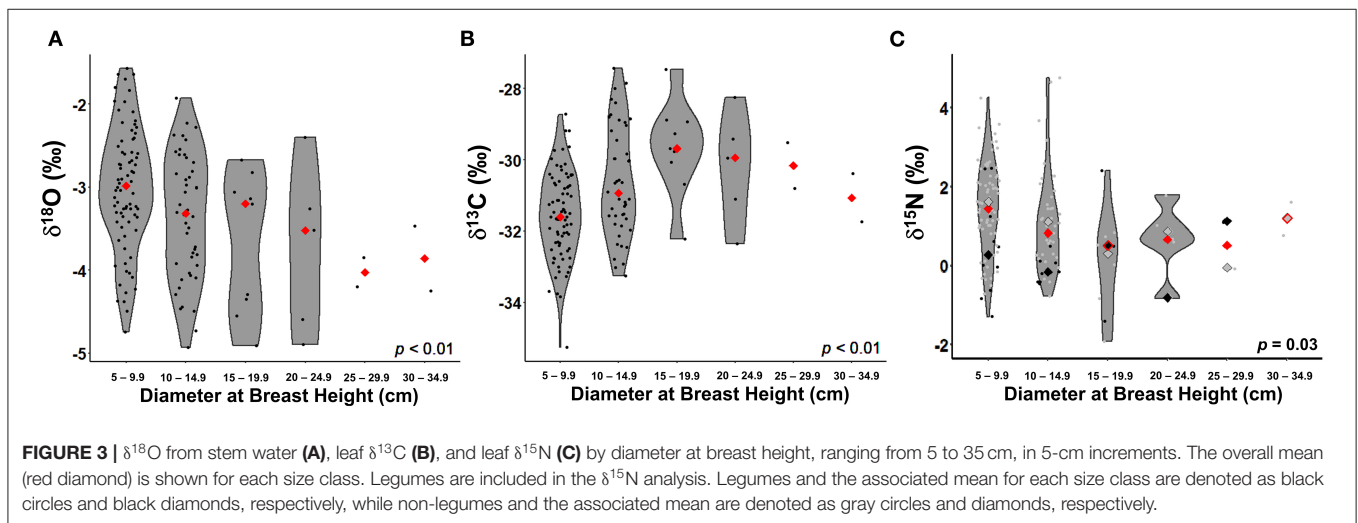
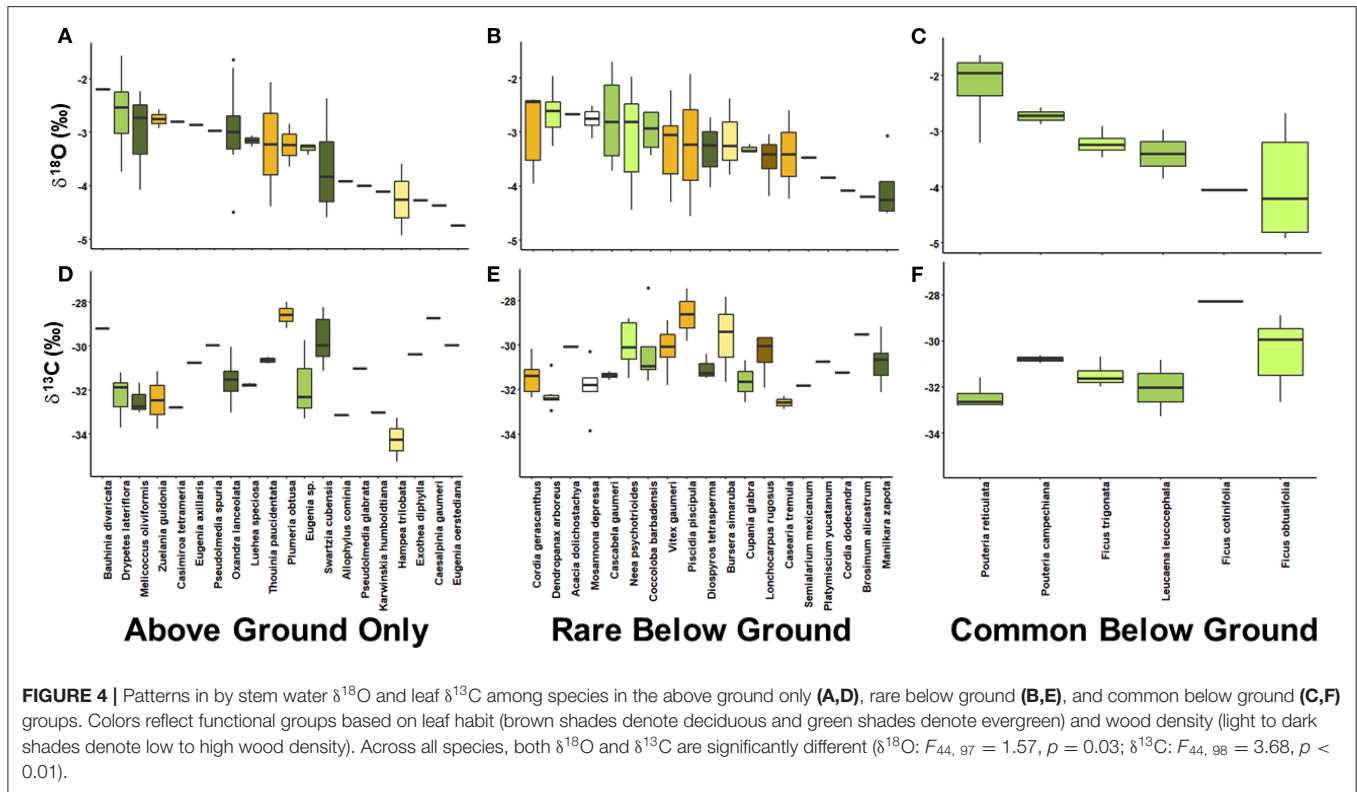


FIGURE 3 | $\delta^{18}\text{O}$ from stem water (A), leaf $\delta^{13}\text{C}$ (B), and leaf $\delta^{15}\text{N}$ (C) by diameter at breast height, ranging from 5 to 35 cm, in 5-cm increments. The overall mean (red diamond) is shown for each size class. Legumes are included in the $\delta^{15}\text{N}$ analysis. Legumes and the associated mean for each size class are denoted as black circles and black diamonds, respectively, while non-legumes and the associated mean are denoted as gray circles and diamonds, respectively.

compared, to only 5 of 15 deciduous species. Therefore, our observations do not support deep rooting specialization by evergreens in general. Rather, our results suggest that evergreen and deciduous species have overlapping root zones with select evergreen species strongly specializing in deep rooting and others (a majority) specializing in shallow rooting. This finding supports observations from other parts of the peninsula that showed no significant division in water sources among deciduous and evergreen species (Querejeta et al., 2007; Hasselquist et al., 2010). A related study on root density in Yucatán found that *B. simaruba*, a deciduous species, had 25% of its roots in the lowest layers of the bedrock (Estrada-Medina et al., 2013a). Studies on tropical tree seedlings from Bolivia found that the majority of deciduous species had taproots compared to evergreen species (Poorter and Marksteijn, 2008). Further, an investigation of root growth into bedrock under irrigation treatments found that deciduous species responded to drought by increasing root growth into rock fractures (Nie et al., 2017). While these observations were on seedlings in greenhouses, they suggest that deciduous species may have aggressive root foraging strategies, which appear to persist as trees age. These

findings combined with our observations suggest that deciduous species are capable of rooting deeply, alongside evergreens in Quintana Roo.

Our findings contrast those from other tropical forests in Venezuela and Panama, which found that evergreens had evidence of deeper water use from water potential measurements and stable isotope assessments (Sobrado, 1986; Jackson et al., 1995; Meinzer et al., 1999). Research on root biomass in Bolivia found that drought-delaying species with conservative traits had deeper root systems compared to acquisitive species (Marksteijn and Poorter, 2009). A potential explanation for this discrepancy may relate to deeper soils in these forests, providing more opportunities for vertical partitioning compared to a karst system, which limits root exploration to pre-existing conduits (Schwinning, 2010; Gao et al., 2016). Therefore, our findings challenge assumptions about rooting depth made from expectations based on leaf habit (Eamus, 1999). Overall, these findings show that multiple species, across leaf habit groups, have potential to access deep water sources in Quintana Roo. Further work on traits that may favor deep rooting specialization in these two groups is warranted.



Tree Size Influences Water Access and Use

Our results showed that tree size was related to water use and water use efficiency. A negative correlation between $\delta^{18}\text{O}$ values of extracted stem water and tree size confirmed that larger individuals utilized deep water more than smaller individuals. The $\delta^2\text{H}$ of stem water exhibited the same patterns, but the correlation was only marginally significant (see **Supplementary Table 6**). This may be explained by relatively small differences in sensitivity to soil conditions or extraction methodologies between $\delta^{18}\text{O}$ and $\delta^2\text{H}$ (Barbata et al., 2019, 2020; Chen et al., 2020; Allen and Kirchner, 2021; Miguez-Macho and Fan, 2021; Nehemy et al., 2022), although more work is needed in this area. Individuals in the two largest size classes were represented by *M. zapota*, *F. trigonata*, *B. alicastrum*, and *L. leucocephala*, which all had roots present in the caves, with *Ficus* spp. and *L. leucocephala* being common below ground. While both are evergreen, *Ficus cotinifolia* Kunth was found to have shallow water use in a previous study (Querejeta et al., 2007) and *L. leucocephala* has been noted as having a more isohydric water use strategy, which might suggest conservative water use and shallower rooting (Liang and Zhang, 1999). *M. zapota* and *B. alicastrum* are notable species in mature forests (García-Frapolli et al., 2007) and important to Maya agroforestry, suggesting deep water access may contribute to their persistence during dry periods (Querejeta et al., 2006; Sánchez-Sánchez et al., 2015); however, limited studies have been conducted on water use strategies of these key species (Benjamin et al., 2001; Querejeta et al., 2006). Our findings agree with studies that show, in general, below ground biomass positively correlates with above ground

biomass (Schenk and Jackson, 2002; Casper et al., 2003), leading to deeper water use compared to smaller trees with shallower root penetration (Sayer and Newbery, 2003; Hasselquist et al., 2010; Phillips et al., 2010).

Our results further suggest that leaf N isotopes provide insight into rooting depth and complement tree water source information from water isotope results in this system. In seasonally dry systems, with increased denitrification in surface layers and leaching with high mean annual precipitation in tropical systems (Pataki et al., 2008; Craine et al., 2015; Roa-Fuentes et al., 2015; Campo, 2016), shallow soils may be expected to have available N with higher $\delta^{15}\text{N}$ values. In addition, in karst soils, N can bind to organic matter in the presence of Ca from the calcium carbonate bedrock (Clarholm et al., 2015; Pan et al., 2016). This decreases plant available N, which may be exacerbated with increasing depth and decreasing soil within bedrock conduits from the surface. Therefore, the smallest trees appear to be accessing shallow sources, as evidenced by relatively heavy-isotope enriched $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$ values. Observed depletion of $\delta^{15}\text{N}$ from the 5 to 9.9 cm DBH group to the 15 to 19.9 cm DBH group may be the result of reduced N availability from leaching and stabilization in soil organic matter at depth. It is crucial to note that the legumes are not driving the depletion among the 15 to 19.9 cm DBH group, as evidenced by a comparable mean $\delta^{15}\text{N}$ among legumes and non-legumes in this DBH class, even though this size class had the highest fraction of legumes represented. Overall, leaf $\delta^{15}\text{N}$ appears to indicate rooting depth, providing further support for water access and utilization among individuals of different sizes in our study.

Interestingly, this relationship with tree size and water use does not correspond to other studies conducted in the Yucatán Peninsula. Similar investigations utilizing stable isotopes report no relationship between water source depth and tree size (Querejeta et al., 2006, 2007; Hasselquist et al., 2010; Estrada-Medina et al., 2013b). Rather, it was previously noted that deep water use by small individuals, particularly deciduous species, may be a critical water use strategy during early life stages (Meinzer et al., 1999; Stratton et al., 2000; Hasselquist et al., 2010). Establishing deep roots with reliable water access early on has been suggested to increase survival in seasonally dry environments (Paz et al., 2015). Individuals in the two smallest size classes in our study expressed the full range of $\delta^{18}\text{O}$ values observed, suggesting more complexity in water use and access, not easily explained by simple variables like tree size. At the same time, our results do suggest that with increasing tree size, variation decreases, with the largest trees relying more heavily on deeper water as a group during the dry season.

Deep Water Use Does Not Equate to Lower Water Use Efficiency

Comparing $\delta^{13}\text{C}$ to cross-sectional area of individual trees showed an increase in $\delta^{13}\text{C}$ values with tree size until a threshold, after which $\delta^{13}\text{C}$ then appeared to decline. This suggests that water use efficiency increases with tree size (suggesting increasing water limitation) until trees reach a certain size, seemingly around 20 cm in diameter in our system, after which efficiency declines (suggesting a concomitant decline in water limitation). As previously discussed, we interpreted the water isotope results as indicating deeper water use by larger trees. We would expect, then, that deeper water access would result in a more stable water source and that would yield lower water use efficiency with increasing tree size. However, this is not the pattern observed. This suggests that while deep water use increases with tree size, complimentary decrease in water use efficiency is not observed until the tree reaches a certain size, suggesting that water limitation in fact increases for all but the very largest trees. We noted that the corollary to this is that smallest trees, without deep water use, had comparable $\delta^{13}\text{C}$ values to the largest trees. This seems surprising as previous work showed that thin top soil and heterogenous conduits in the bedrock affect the spatial distribution of water in these karstic systems (Estrada-Medina et al., 2013a). Studies from the Edwards Plateau in Texas, USA have shown that evapotranspiration and soil moisture tended to be dynamic near the surface, suggesting short-term and readily depleted soil water storage (McCole and Stern, 2007; Heilman et al., 2014). Yet, the smallest trees (5–9.9 cm DBH) in our system utilizing shallow water appear to withstand these fluctuations in water availability, potentially because the lower water demands by small trees are being met by the soil-filled voids in the limestone (Schwartz et al., 2013; Ding et al., 2018, 2021). On the other hand, medium sized trees (15–19.9 cm DBH and 20–24.9 cm DBH) display high water use efficiency and potential water stress, as their relatively higher water demands are apparently not being satisfied by often low and variable water in the pores. The observed patterns in water use and water use

efficiency highlights the range of strategies and suggests that tree size is important to consider when evaluating water use and strategies among co-occurring species. Furthermore, there may be implications for how size distribution among species and with communities may impact responses to disturbance and climate change.

Functional Groups Mask Relevant Species-Specific Water Use Strategies

We predicted that functional groups would inform water use strategies among species in these semi-evergreen tropical forests. Yet, the functions we observed inferred from stable isotopes and direct root observations were not well-predicted by existing groups for these dry tropical forest species. While the functional group framework has been useful for predicting vegetation responses to environmental change (Lavorel and Garnier, 2002; Poorter and Bongers, 2006; Sterck et al., 2006; Maire et al., 2015), some studies in seasonal tropical systems have found that organizing species based on a few leaf or wood traits does not explain variation in responses to water limitation. For example, a study from a tropical dry forest in Costa Rica showed that canopy position and leaf toughness explained variation in leaf $\delta^{13}\text{C}$ while leaf habit did not (Leffler and Enquist, 2002). In our study, significant variation within groups resulted in a lack of variation between groups, similarly observed by Powers and Tiffin (2010). Therefore, evaluating water use strategies by functional groups masks relevant species variation that could impact community composition and ecosystem functioning, particularly in diverse tropical regions.

CONCLUSIONS

The karst topography of the Quintana Roo provided the unique opportunity to evaluate water use strategies among co-occurring species and functional groups through above and below ground observations. Through direct root observation in caves, we showed that rooting depth does not match predictions based solely on functional groups. Evergreen and deciduous species were observed rooting together with overlapping root zones and in fact, a higher fraction of deciduous species appeared to access groundwater than evergreen, although all the species dominant in the caves were evergreens. This finding implies that there is competition for resources and potentially space in the limestone in Quintana Roo and karst landscapes in general. Future work should work to characterize the bedrock matrix as well as soil water content and associated stable isotope values to better describe water availability, water use, and competition within the epikarst. Rooting depth and root abundance did not predict water use efficiency, suggesting that some species can manage resources effectively, even without deep water access. Differences in water use and water use efficiency was better explained by tree size. Progressively larger trees were utilizing deep water, but the trees in the smallest DBH size class had overlapping $\delta^{13}\text{C}$ values with trees in the largest DBH size class, suggesting water demands of the small individuals were being met by water in shallow soils and bedrock while large trees were successfully accessing

groundwater to increase plant performance. This relates to differences among successional stages, with implications for how size distribution among species and within communities may impact responses to disturbance and climate change. Further studies within the region will not only increase sample size but include a wider distribution of tree sizes and species to capture broader community-level patterns. Finally, functional groups did not accurately depict water use strategies among co-occurring species. This framework appears to mask relevant species variation, as observed among the abundant species, that could impact community composition and ecosystem functioning in this seasonally dry region. Therefore, research on species-specific resource acquisition strategies and ecophysiological responses to water availability needs to be on the forefront to properly assess the trajectories of these and other seasonally dry tropical forests in future climate scenarios.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

RA and JW designed the research, conducted fieldwork, and wrote the manuscript. RA performed experiments and analyzed

data. Both authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/frwa.2022.950346/full#supplementary-material>

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