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# Water source partitioning among trees growing on shallow karst soils in a seasonally dry tropical climate

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**Abstract** The sources of water used by woody vegetation growing on karst soils in seasonally dry tropical regions are little known. In northern Yucatan (Mexico), trees withstand 4–6 months of annual drought in spite of the small water storage capacity of the shallow karst soil. We hypothesized that adult evergreen trees in Yucatan tap the aquifer for a reliable supply of water during the prolonged dry season. The naturally occurring concentration gradients in oxygen and hydrogen stable isotopes in soil, bedrock, groundwater and plant stem water were used to determine the sources of water used by native evergreen and drought-deciduous tree species. While the trees studied grew over a permanent water table (9–20 m depth), pit excavation showed that roots were largely restricted to the upper 2 m of the soil/bedrock profile. At the peak of the dry season, the $\delta^{18}O$ signatures of potential water sources for the vegetation ranged from $4.1 \pm 1.1‰$ in topsoil to $-4.3 \pm 0.1‰$ in groundwater. The $\delta^{18}O$ values of tree stem water ranged from $-2.8 \pm 0.3‰$ in *Talisia olivae-formis* to $0.8 \pm 1‰$ in *Ficus cotinifolia*, demonstrating vertical partitioning of soil/bedrock water among tree species. Stem water $\delta^{18}O$ values were significantly different from that of groundwater for all the tree species investigated. Stem water samples plotted to the right of the meteoric water line, indicating utilization of water sources subject to evaporative isotopic enrichment. Foliar $\delta^{13}C$ in adult trees varied widely among species, ranging from $-25.3 \pm 0.3‰$ in *Enterolobium cyclocarpum* to $-28.7 \pm 0.4‰$ in *T. olivaeformis*. Contrary to initial expectations, data indicate that native trees growing on shallow karst soils in northern Yucatan use little or no groundwater and depend mostly on water stored within the upper 2–3 m of the soil/bedrock profile. Water storage in subsurface soil-filled cavities and in the porous limestone bedrock is apparently sufficient to sustain adult evergreen trees throughout the pronounced dry season.

**Keywords** Yucatan · Isotopes · Resource partitioning · Groundwater · Rooting depth

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## Introduction

Vegetation types differ widely in vertical root distributions and maximum rooting depth (Canadell et al. 1996; Schenk and Jackson 2002). Rooting depths are correlated with aboveground plant size, as shrubs and trees are 4–6 times more likely to have roots reaching depths ≥4 m than semi-shrubs and herbaceous plants (Schenk and Jackson 2005). The probability of deep

rooting is also strongly related to climate variables that affect soil water balance. Deep rooting is mainly found in temperate and tropical water-limited ecosystems dominated by woody vegetation. According to current empirical models, deepest rooting depths (both average and maximum) are most likely to occur in seasonally dry tropical regions with high transpiration demand during dry seasons (Schenk and Jackson 2005). Comparisons between the seasonal surplus of water during the wet season and the potential evaporative demand during the dry season suggest that in highly seasonal tropical climates, use of deeply stored soil water could potentially account for 1–6 months of ecosystem transpiration during dry seasons. However rooting depth in shallow, rocky karst soils might differ significantly from model predictions, as there are very few empirical data on root distribution from karst regions (Schenk and Jackson 2005). Deep sampling can be extremely labor demanding in karst soils with shallow bedrock, which may explain the lack of data in the literature. Although shallow bedrock hampers the downward growth of roots in karst soils (Duch 1991), weathered limestone bedrock often allows root penetration through a network of cracks, fissures and channels (Canadell et al. 1996). The roots of some plant species have even been found to penetrate directly through calcareous bedrock in Mediterranean-type ecosystems (Oppenheimer 1958). Shallow limestone bedrock might or might not invalidate model predictions regarding rooting patterns and depth of water uptake by plants in dry tropical karst areas such as the Yucatan peninsula of Mexico.

The Yucatan peninsula is a low-lying karst platform characterized by shallow soils underlain by limestone (Weidie 1985; Duch 1991, 1995). Despite very limited soil water storage capacity (Weisbach et al. 2002), plants must endure 4–6 months of drought per year in the strongly seasonal dry tropical climate of northern Yucatan (Orellana et al. 1999). Rooting depth in the tropics is negatively correlated with annual precipitation and positively correlated with the length of the dry season (Schenk and Jackson 2002), all of which indicate that deep rooting may be functionally important for woody vegetation in northern Yucatan. Some native tree species frequently found in traditional non-irrigated agroforestry systems in northern Yucatan maintain their foliage throughout the dry season, suggesting that they might have access to permanent sources of water (Benjamin et al. 2001). While most native woody species in northern Yucatan are drought deciduous, many of them flush new leaves during the dry season, which also hints at root access to moist subsoil layers or groundwater. Northern Yucatan is

underlain by a permanent groundwater table within 5–20 m of the land surface (Socki et al. 2002). There are numerous examples in the literature of woody plants sending roots to water tables at similar or greater depths (Lewis and Burghy 1964; Canadell et al. 1996 and references therein; Zencich et al. 2002; Gries et al. 2003; Ludwig et al. 2003). It is therefore often assumed that adult evergreen trees in Northern Yucatan tap the aquifer during the dry season (Benjamin et al. 2001).

The zones of active water uptake by plant roots have traditionally been difficult to determine, but analyses of hydrogen and oxygen stable isotope ratios at natural abundance have enabled researchers to more accurately discriminate among different potential water sources (Ehleringer and Dawson 1992; Brunel et al. 1995). In tropical regions the isotopic signature of rainfall water often exhibits little seasonal variation compared to temperate continental areas (Yurtsever and Gat 1981), and a pronounced dry season may be required for the development of vertical gradients in the isotopic composition of soil water. During the dry season, the upper soil layers become enriched in the heavier isotopes (D and $^{18}$O) due to evaporative fractionation, resulting in steep gradients in oxygen and hydrogen isotopic signatures with depth (Barnes and Turner 1998). In the Yucatan the isotopic composition of soil water is expected to be most distinct from that of groundwater at the peak of the dry season, as the aquifer is not subject to evaporative enrichment (Socki et al. 2002). Phreatophytic plants may use soil water during wet periods, but they generally switch to groundwater sources as the soil dries out (e.g., Zencich et al. 2002). Therefore xylem sap isotopic signatures of phreatophytic and shallow-rooted tree species are expected to differ most widely from each other during the dry season.

We hypothesized that mature individuals of evergreen tree species growing on thin soils over karst would tap the aquifer for a reliable supply of water during the dry season, thus circumventing the problem of limited soil water storage. The naturally occurring concentration gradients in oxygen and hydrogen stable isotopes in soil, bedrock, groundwater and stem water were used to investigate the sources of water used by both evergreen and drought-deciduous tree species at the peak of drought. Leaf $\delta^{13}$C was also measured because this parameter reflects the interplay among all aspects of plant carbon and water relations (Dawson et al. 2002), and therefore can be used to explore the range of interspecific variation in water use efficiency and water use strategy (Bonal et al. 2000; Franco et al. 2005).

## Materials and methods

### Site description

The study was carried out in three neighbouring locations in northern Yucatan with agroforest vegetation: Kampepén, Santa Cruz, and Hocabá. Hocabá (089°14′42″W, 20°48′56″N) is a traditional mixed agroforest system, Santa Cruz (089°39′12″W, 20°52′45″N) is a former hacienda (agricultural estate) and Kampepén (089°39′10″W, 20°50′00″N) is an hacienda under cultivation. These experimental sites are 4–30 km apart from each other. Climatic and physiographic conditions are very similar at the three sites. Average annual temperature is 27.2°C, and total annual precipitation is approximately 1,000 mm. The rainy season normally extends from May through October. The area experiences a pronounced 4- to 6-month dry season in the winter/spring months during which only about 10–20% of the total annual rainfall is received (Orellana et al. 1999). Mean temperatures during the dry season range from 22.5°C in January to 27.4°C in April, although mean maximum daily temperatures reach 36°C at the peak of drought in April. Minimum average daily temperatures during the dry season range from 17.9°C in January to 21.5°C in April. Elevation above sea level is 10 m at Kampepén and Santa Cruz and 14 m at Hocabá. The topography of northern Yucatan is mostly flat, and the lithology consists of highly permeable Tertiary limestones and dolomites (Weidie 1985). Soils are very shallow and rocky (Duch 1991, 1995; Estrada-Medina 2000), and are classified as Lithic (Kampepén) or Skeletal (Hocabá and Santa Cruz) Leptosols according to the FAO system. Organic matter content is very high in these soils, ranging from 23.5 to 49.9% (Bautista-Zuñiga et al. 2004). Soil water content at field capacity (−0.03 MPa) ranges from 40 to 65% of dry soil weight in these soils. Moisture content at wilting point (−1.5 MPa) ranges from 33 to 59% of dry soil weight. Therefore plant-available water (the difference between moisture content at field capacity and permanent wilting point) is only 2–12% in these soils (Weisbach et al. 2002). A very hard limestone layer formed by the solution and precipitation of calcium carbonate (locally known as "laja"; Duch 1991, 1995; González-Herrera et al. 2002) is found at or near the ground surface in northern Yucatan. Below the shallow soil and hard capping surface layer there is a softer, friable limestone with spongy texture which is locally termed "sascab". Subsurface sascab strata can be several meters thick in northern Yucatan (Estrada-Medina et al. 2005). Meteoric precipitation infiltrates quickly into the porous, permeable limestone bedrock

(González-Herrera et al. 2002). Depth to the groundwater table is 9 m at Kampepén and Santa Cruz and 20 m at Hocabá, with small (<1 m) interseasonal fluctuations.

The mixed agroforests in the three experimental areas have a high diversity of native tree species and show a forest-like structure, with interspersed individuals of different species and age. The seven native tree species selected for the study included representatives of six different plant families (Table 1). These species have contrasting leaf habits and adult tree size, and are all key components of both natural forests and traditional mixed agroforests in the Yucatan peninsula (Xuluc 1995).

### Sampling

Plant and soil/bedrock sampling was conducted simultaneously at the three experimental sites in late April 2002 (late dry season). The number of trees sampled per species and per site are described in Table 1. Suberized twigs approximately 10 mm in diameter and 50–80 mm long were cut from the canopy, and all leaves and green stem tissue were removed from them to avoid contamination of xylem water by isotopically enriched water (Ehleringer and Dawson 1992). Two stem samples were collected per tree. Clipped twigs were immediately placed in a capped vial, wrapped in parafilm and stored in the freezer until water extraction. Surface (0–10 cm) soil samples were collected using a hand-driven probe for water content determination and stable isotope analyses of soil water. Pits were excavated in order to characterize all possible sources of water for plants during the dry season. One pit 1.5–2 m in diameter was excavated at each of the three study sites in late April 2002. The pits were manually excavated by three different teams of local Maya well drillers using picks and shovels and dynamite. All the three pits were made within 2–3 m of the base of a *Brosimum* tree to get a rough estimate by visual inspection of average and maximum rooting depths in this and neighboring species. Pits were dug down to a depth of 4 m in Hocabá and Santa Cruz, or until the groundwater table was reached in Kampepén (9 m depth). Soil/bedrock samples were promptly taken from freshly excavated pit sidewalls for water content measurement and for stable isotope analysis of water. Soil and bedrock samples were collected at least 5 cm deep (horizontally) into the sidewalls of the pits to avoid alteration of water isotopic composition by evaporative enrichment during the process of excavation. The irregular spatial distribution of soil pockets and sascab bedrock strata in the soil/bedrock profiles

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**Table 1** Characteristics of the tree species selected for foliar $\delta^{13}C$ measurements and for $\delta D$ and $\delta^{18}O$ analyses of xylem water[a]. *DBH* Diameter at breast height

| Species | Family | Common names (Spanish/Maya) | Number of adult trees sampled | DBH (cm) | Leaf phenology | Leaf $\delta^{13}C$ (‰) | Peak leaf fall |
|---|---|---|---|---|---|---|---|
| *Cedrela odorata*[b] | Meliaceae | Cedro/Kulché | 4 | 30–49 | Deciduous | $-25.5 \pm 0.3$ | December–February |
| *Spondias purpurea*[b] | Anacardiaceae | Ciruelo/Abal | 4 | 39–70 | Deciduous | $-26.5 \pm 0.2$ | January–May |
| *Cordia dodecandra*[c] | Boraginaceae | Ciricote/Copte | 4 | 38–42 | Subdeciduous | $-27.5 \pm 0.6$ | February–May |
| *Enterolobium cyclocarpum*[d] | Leguminosae | Parota/Pich | 3 | 71–95 | Deciduous | $-25.3 \pm 0.3$ | January–May |
| *Brosimum alicastrum*[e] | Moraceae | Ramón/Ox | 10 | 32–99 | Evergreen | $-28.6 \pm 0.6$ | – |
| *Talisia olivaeformis*[f] | Sapindaceae | Huaya/Wayum | 3 | 32–59 | Evergreen | $-28.7 \pm 0.4$ | – |
| *Ficus cotinifolia*[g] | Moraceae | Álamo/Kopó | 3 | 45–79 | Evergreen | $-27.2 \pm 0.7$ | – |

[a] Leaf $\delta^{13}C$ and xylem water $\delta D$ and $\delta^{18}O$ were measured at the peak of drought in April 2002

[b] All four trees were sampled at the Hocabá site

[c] Two trees were sampled at the Hocabá site and another two trees at the Kampepén site

[d] Two trees were sampled at Kampepén and another one at Santa Cruz

[e] Four trees were sampled at Kampepén, another three at Hocabá, and three more at Santa Cruz

[f] Two trees were sampled at Kampepén and another one at Hocabá

[g] One tree was sampled at each of the three experimental sites

prevented sampling at precisely regular depth intervals. Samples were taken at approximately 10- to 15-cm increments in the 0- to 50-cm-depth interval, every 30–50 cm in the 50- to 200-cm-depth interval, or every 100 cm at 200–400 cm. At each depth, two replicate soil/bedrock samples were collected from two opposite sidewalls of the pit. Freshly collected soil and bedrock samples were placed in capped vials, wrapped in parafilm and stored in the freezer until water extraction for stable isotope analyses. Groundwater samples were obtained from nearby wells in Hocabá, Kampepén and Santa Cruz, as well as from the pit excavated in Kampepén. Additionally, we interviewed ten different local well drillers to enquire about typical root distributions and maximum rooting depths encountered during extensive professional practice in the experimental area.

Water was extracted from soil and plant stem samples using a cryogenic vacuum distillation line (Ehleringer et al. 2000). The water content of soil and bedrock samples was calculated according to differences in sample weight before and after thorough water extraction (100°C, 3 h). Oxygen and hydrogen stable isotope analyses were conducted at the Center for Stable Isotope Biogeochemistry of the University of California at Berkeley. $\delta^{18}O$ values were obtained by the $CO_2:H_2O$ equilibration method: 500 µl of the extracted water was injected into airtight vials flushed with 2,000 or 3,000 p.p.m. $CO_2$ in He. After 48 h, $CO_2$ in the head space was analyzed for its oxygen isotope ratio with a Finnigan MAT Delta Plus XL isotope mass spectrometer (IRMS) interfaced with a GasBench II

and PAL-80 autosampler (Tu et al. 2001). $\delta D$ analyses were conducted on a subset of water samples using a chromium reactor on a Finnigan MAT H/Device dual inlet IRMS system. All $\delta^{18}O$ and $\delta D$ values are expressed in delta notation (‰) relative to an accepted international standard (Vienna standard mean ocean water) (Ehleringer and Dawson 1992). Analytical precision was $\pm 0.18$‰ for $\delta^{18}O$ and $\pm 0.7$‰ for $\delta D$.

The proportion of water absorbed from different environmental sources at the peak of the dry season was calculated for each tree species using the Iso-Source mixing model (freely available at http://www.epa.gov/wed/pages/models.htm; Philips and Gregg 2003). This model gives the distribution of proportions of feasible sources when there is a high number of potential sources, and is based solely on isotopic mass balance constraints. We considered four distinct water sources (soil, shallow bedrock, deep bedrock and groundwater) and used both $\delta^{18}O$ and $\delta D$ data for model calculations. Based on rooting depth estimates by visual inspection and on $\delta D$–$\delta^{18}O$ plots (see below), an additional non-isotopic constraint was applied on the model to further reduce the range of numerically feasible contributions from each source (Philips and Gregg 2003). This was done by selecting only those numerically feasible solutions in which the contribution from deep bedrock was equal to or greater than the contribution from groundwater.

In late April 2002, sunlit leaf samples were collected from the trees included in the water source determination study. Leaf material was oven dried, ground and analyzed for $\delta^{13}C$. Analyses were conducted on a

continuous flow mass spectrometer (Europa Scientific Hydra 20/20; Cheshire, UK) at the Stable Isotope Facility of the University of California at Davis. $\delta^{13}C$ values are expressed in delta notation relative to an accepted international standard (Pee Dee Belemnite).

Statistical analyses were conducted using the SPSS 13.0 program. Stem water $\delta^{18}O$ data and leaf $\delta^{13}C$ data were subjected to one-way ANOVA followed by post hoc Fisher's least significant difference test in order to detect significant ($P < 0.05$) differences among tree species.

## Results

Manually-excavated pits revealed a rocky, shallow top-soil (about 5–30 cm deep) overlying heterogeneous fissured bedrock (Fig. 1a–d). A very hard consolidated limestone layer (laja) at or near the ground surface (Fig. 1c) was underlain by softer and more friable bedrock of high porosity and spongy texture (sascab; Fig. 1e). Soil-filled cracks, crevices and cavities (from a few centimeters up to 50 cm in diameter) were found within the limestone bedrock matrix, although they were generally restricted to the upper 1–2 m of the profile. Pit excavation showed that tree roots were mostly concentrated in the upper soil and bedrock layers and were predominantly horizontally oriented (Fig. 1a). Root density in the thin soil layer as well as in soil pockets within the limestone bedrock matrix was extremely high (Fig. 1b). Dense mats of roots were found growing along cracks in the bedrock. Sascab bedrock strata in the upper 2 m of the profile were also colonized by fine roots, although more sparsely so than topsoil and soil-filled cavities (Fig. 1e). Root abundance declined sharply with depth, and no roots could be found below 2 m despite careful visual inspection of pit sidewalls in all the pits. Root access to greater depths appeared to be strongly hampered by the thick limestone shell overlying the water table. This observation is supported by extensive anecdotal evidence gathered by local Maya well drillers with ample experience excavating pits in the area. Ten different experienced well drillers consistently reported that roots are rarely found below 2–3 m depth in northwest Yucatan (personal communication).

Total precipitation during the 12 months preceding sampling in late April 2002 was below normal

**Fig. 1** Pictures taken during excavation of the experimental pits, showing a typically shallow rooting pattern with sharp decline of root density at the soil/bedrock interface in Hocabá (**a**); high density of roots within the thin soil layer in Santa Cruz (**b**); consolidated limestone layer ("laja") found near the surface (5–10 cm depth) in Kampepén (**c**); fissured limestone bedrock (50 cm depth) in Kampepén (**d**); fine root colonizing a weathered bedrock layer ("sascab") in Kampepén (**e**)

(702.6 mm, which is less than 70% of the long-term mean). Less than 9 mm of rain fell during March and April 2002 at the experimental sites. At the peak of drought in late April 2002, the average water content in the soil/bedrock profile was 14.7 ± 1.6% at 10 cm depth, decreased to 10.1 ± 2.2 at 40 cm, and increased again to 13.6 ± 2.7% at 150 cm (Fig. 2). The water content of deeper bedrock decreased with depth, from 10 ± 0.5% at 200 cm to 4.8 ± 1.2% at 400 cm. Large SEs of soil/bedrock mean water content values reflected the extreme heterogeneity of the substrate, characterized by irregularly distributed soil pockets interspersed within a complex matrix of limestone bedrock strata of various porosities. Maximum soil water content was recorded in a subsurface soil-filled cavity found at 70 cm depth in Hocabá (27%). Bedrock water content was highest in sascab limestone strata (up to 12%) at the three sites. Soil water $\delta^{18}O$ values exhibited the expected evaporative enrichment in the heavier isotope near the surface, as the sharply seasonal rainfall distribution of Northern Yucatan's climate favored the development of a steep vertical isotopic gradient in the soil/bedrock profile. Evaporative isotopic enrichment of soil/bedrock water was greatest near the surface but declined sharply with depth (Fig. 3). Soil/bedrock water $\delta^{18}O$ values decreased abruptly from 4.1 ± 1.1‰ at 5 cm to −2 ± 0.4‰ at 40 cm. Bedrock water became progressively depleted in $^{18}O$ between 40 and 200 cm. The $\delta^{18}O$ signature of bedrock water reached similar values to those of groundwater at around 300 cm depth. Aquifer water samples collected from nearby wells at the three experimental sites and from the excavated pit at Kampepén yielded an average $\delta^{18}O$ value of −4.3 ± 0.1‰ (n = 5).

Leaf $\delta^{13}C$ varied widely among species, ranging from −25.3 ± 0.3‰ in *Enterolobium cyclocarpum* to −28,7 ± 0.4‰ in *Talisia olivaeformis* (Table 1). *Cedrela odorata* trees were just initiating leaf flushing at time of sampling, so the extremely enriched twig water $\delta^{18}O$ values that they showed (6–11‰) did not reflect tree water source, but cumulative evaporative enrichment of twig water throughout the dry season (Forstel and Hützen 1983; Philips and Ehleringer 1995). Therefore twig water isotopic data from *Cedrela odorata* were excluded from the water source determination study. The remaining drought-deciduous species initiated leaf flushing several weeks before sampling, so it can be safely assumed that the isotopic composition of their twig water reflected that of water sources. The $\delta^{18}O$ values of twig water ranged from −2.8 ± 0.3‰ in *T. olivaeformis* to 0.8 ± 1‰ in *Ficus cotinifolia*, indicating vertical partitioning of water sources during the dry
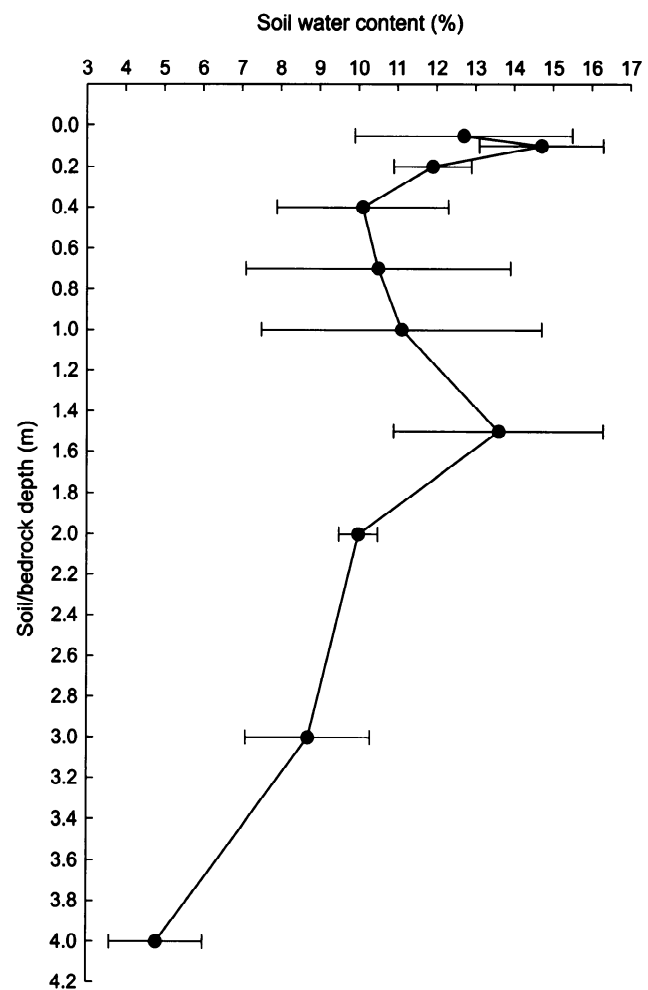


**Fig. 2** Soil/bedrock water content, showing average means and SEs of three profiles collected at Hocabá, Santa Cruz and Kampepén (n = 3, except for n = 11 at 5 cm depth and n = 6 at 10 cm depth)

season (Fig. 3). Water uptake appeared to be largely restricted to the upper soil layers in *F. cotinifolia, Cordia dodecandra* and *Spondias purpurea*, while *Brosimum alicastrum, E. cyclocarpum* and *T. olivaeformis* were absorbing a greater proportion of deep water sources. Stem water $\delta^{18}O$ values were significantly different from groundwater for all the tree species investigated (P < 0.001; Mann–Whitney U-test). Groundwater $\delta^{18}O$ and $\delta D$ values plotted on the meteoric water line (MWL; Socki et al. 2002), as shown in Fig. 4. Stem water samples deviated to the right of the MWL even for the three tree species with the least isotopically enriched xylem sap, indicating utilization of water sources subject to evaporative isotopic enrichment (Williams and Ehleringer 2000). The tree species with the least isotopically enriched stem water exhibited $\delta^{18}O$ and $\delta D$ values that either closely matched those of bedrock water (*T. olivaeformis*), or plotted near the line between bedrock water and soil water
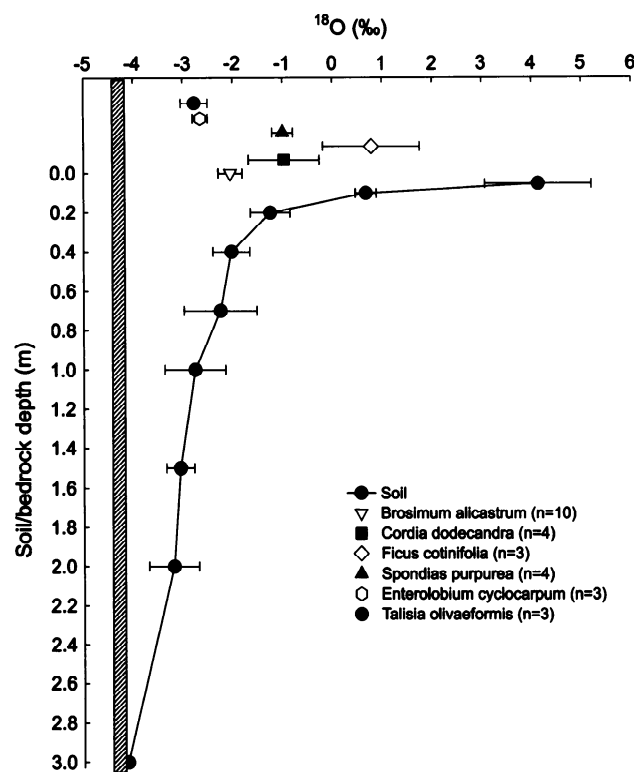
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**Fig. 3** Average $\delta^{18}O$ isotopic profile of soil/bedrock water and $\delta^{18}O$ values of stem water (mean ± SE) in six different tree species at the peak of the dry season in late April 2002. Soil/bedrock values represent means and SEs of three different profiles, each collected at one of the study locations ($n$ = 3, except for $n$ = 6 at 5 and 10 cm depths). The *bar* represents the $\delta^{18}O$ value of groundwater



**Fig. 4** $\delta D$ vs. $\delta^{18}O$ values from *Brosimum*, *Enterolobium* and *Talisia* adult trees, soil water, bedrock water and groundwater in April 2002 in three non-irrigated Maya agroforestry systems in northern Yucatan. *Fitted line* is the meteoric water line ($\delta D$ = 8.11 × $\delta^{18}O$ + 10.4; Socki et al. 2002)

(*E. cyclocarpum* and *B. alicastrum*) (Fig. 4). There was a relatively wide range of combinations of numerically feasible sources which could explain the isotopic composition of stem water in each tree species, because the large number of distinct water sources in the system precluded unique solutions (Table 2).

## Discussion

Contrary to initial expectations, none of the tree species investigated showed stem water $\delta^{18}O$ values which might suggest heavy reliance on groundwater during the dry season. Phreatophytic species typically exhibit xylem sap isotopic values closely matching that of aquifer water, particularly during drought periods when other sources of water are scarce or depleted (Flanagan et al. 1992; Ewe et al. 1999; Snyder and Williams 2000; Zencich et al. 2002; Chimner and Cooper 2004). In our study, average stem water $\delta^{18}O$ signatures at the peak of the dry season were between 1.5 and 5.1‰ more enriched than that of aquifer water, depending
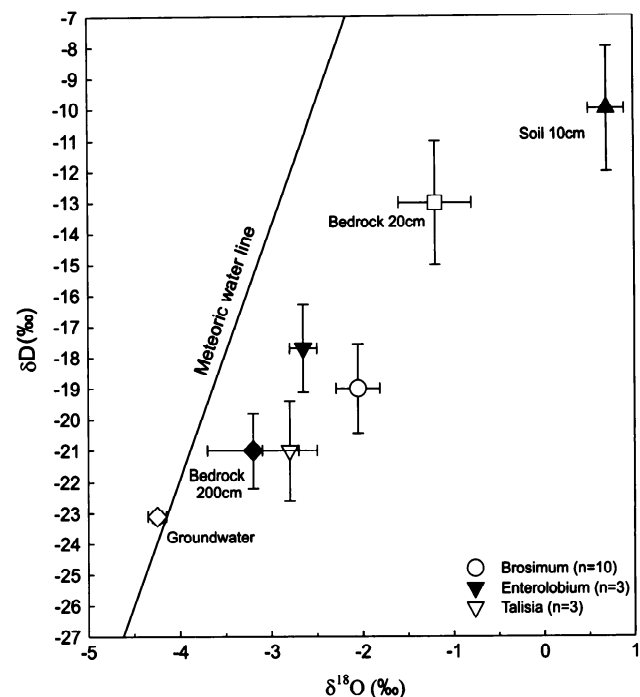
on tree species. The results yielded by the IsoSource model (Table 2) indicated that the tree species investigated used little or no groundwater (0–11% on average) during the dry season. In another tropical karst region with shallow soils and seasonally dry climate (the Lower Florida Keys), Ish-Shalom et al. (1992) also found that hammock tree species primarily utilized soil water and not aquifer water. Conversely, hammock vegetation in mainland Florida utilized a substantial amount of groundwater during the dry season, although depth to the aquifer was only 0.6–1.5 m (Ewe et al. 1999). Groundwater utilization by woody vegetation under seasonally dry climates has often been shown to decrease with depth to the phreatic level, even when substrates overlying the aquifer are much easier to penetrate by roots than limestone bedrock (Farrington et al. 1996; Cramer et al. 1999; Zencich et al. 2002).

According to IsoSource model calculations, the tree species investigated were rather dependent on water stored within the bedrock during the dry season (Table 2). It was estimated that the tree species with the least isotopically enriched xylem sap (*B. alicastrum*, *T. olivaeformis* and *E. cyclocarpum*) derived around 80–89% of their water from bedrock sources at the peak of the dry season. Even the tree species with the

**Table 2** Proportions of feasible water sources (%)[a] for the different tree species at the peak of the dry season in late April 2002. Only species for which both $\delta^{18}O$ and $\delta^2H$ data from at least three adult trees were available were used for the calculations (sampling scheme is described in detail in Table 1). Average source proportions calculated by the model are shown, as well as the range of minimum/maximum source proportions (*in parentheses*)

| | F. cotinifolia | S. purpurea | C. dodecandra | E. cyclocarpum | B. alicastrum | T. olivaeformis |
|---|---|---|---|---|---|---|
| Soil (0–15 cm)[b] $\delta^{18}O = 2‰, \delta D = -5‰$ | 86.8 (76–98) | 76.6 (59–87) | 58.6 (26–80) | 8.7 (0–28) | 6.5 (0–24) | 2.8 (0–12) |
| Shallow bedrock (15–70 cm)[b] $\delta^{18}O = -1.2‰, \delta D = -13‰$ | 7.8 (1–23) | 15 (1–40) | 24.2 (1–73) | 29.3 (1–66) | 25.6 (1–55) | 15.1 (1–33) |
| Deep bedrock (70–300 cm)[b] $\delta^{18}O = -3.2‰, \delta D = -21‰$ | 4.5 (1–12) | 7 (1–17) | 13.9 (1–37) | 50.7 (18–93) | 56.5 (23–99) | 73.9 (35–99) |
| Groundwater $\delta^{18}O = -4.3‰, \delta D = -23‰$ | 0.8 (0–4) | 1.4 (0–5) | 3.3 (0–13) | 11.2 (0–32) | 11.3 (0–32) | 8.2 (0–32) |

[a] Water source proportions were calculated using the IsoSource model (http://www.epa.gov/wed/pages/models.htm, Philips and Gregg 2003), after introducing the additional non-isotopic constraint of greater contribution from bedrock water than from groundwater sources (see Results)

[b] Soil/bedrock water isotopic values represent average values of depth intervals specified in the table

most isotopically enriched xylem sap (*F. cotinifolia, S. purpurea* and *C. dodecandra*) drew around 13–38% of their water from the bedrock, although the thin soil layer was the major source of moisture for these species. The critical role that bedrock water plays in supporting tree transpiration during dry periods in ecosystems with shallow soils is well established (e.g., Zwieniecki and Newton 1996; Hubbert et al. 2001; Rose et al. 2003). Weathered bedrock has many physical characteristics that enable it to serve soil-like functions, such as high porosity, saturated hydraulic conductivity and water holding capacity (Rose et al. 2003). Assuming that the entire soil/bedrock profile is recharged during the rainy and hurricane seasons (June–November) in the Yucatan, the total volume of plant-available water held within the bedrock could be substantially greater than that held within the soil, because layers of weathered bedrock (sascab) are much thicker than the overlying soils. Further, subsurface soil-filled cavities within the limestone bedrock matrix can hold large volumes of water which are better protected from evaporative loss than surface soil water. One hundred and forty millimeters of rain fell during the dry season (November 2001–April 2002) at the experimental sites, which was apparently enough to prevent excessive desiccation of the upper layers of the soil/bedrock profile. Several other studies conducted in seasonally dry tropical ecosystems have also concluded that trees depend mostly on water stored within the upper 1–4 m of the soil/subsoil profile during the dry season (Jackson et al. 1999; Stratton et al. 2000; Sternberg et al. 2002), including sites where shallow (2–4 m) groundwater is available (Drake and Franks 2003). Conversely, Oliveira et al. (2005) reported extensive depletion by trees of soil water stored at 4–7.5 m depth in a Brazilian dry tropical forest during dry periods.

Nepstad et al. (1994) and Jipp et al. (1998) also found substantial tree water uptake at depths greater than 8 m in an evergreen tropical forest in eastern Amazonia.

Stem water $\delta^{18}O$ data demonstrated vertical partitioning of water sources among tree species during the dry season. Partitioning of water resources may favor species coexistence and thus could play a role in maintaining a high taxonomic diversity in natural forests and traditional mixed agroforests of northern Yucatan. Different rooting habits or differential ability to grow roots into bedrock are two possible mechanisms that may explain vertical partitioning of water among species. Greater lateral spread of roots or higher density of roots in the thin soil layer could compensate for limited ability to access water stored within the limestone bedrock in shallow rooted species. Conversely, competitive exclusion of roots from the thin soil layer by neighboring trees may lead to heavier reliance on water stored in the bedrock in certain tree species. Aside from differences in rooting patterns, species-specific differences in root activity with depth are also possible, as tree species may have different water requirements or different water use strategies which may influence depth of water uptake. It is interesting to note that water source partitioning among species in our study was not merely the result of interspecific differences in tree size, as xylem sap $\delta^{18}O$ was not correlated with tree diameter (data not shown). Jackson et al. (1999) hypothesized that rapid development of deep roots to reach soil layers where substantial water depletion does not occur may facilitate establishment and survival of small trees in seasonally dry tropical ecosystems. Our results also point to the absence of a pronounced influence of plant size on water uptake depth, strongly supporting Jackson et al.'s (1999) hypothesis.

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Contrary to initial expectations, we found no clear relationship between tree leaf phenology and water acquisition depth as inferred from $\delta^{18}O$ data. The seemingly intuitive assumption that evergreen tree species tap deeper sources of water whereas drought-deciduous ones obtain water from shallower soil layers (Jackson et al. 1995; Meinzer et al. 1999) was not fully supported by the data. While the evergreen *F. cotinifolia* was absorbing water mostly from the shallowest soil/bedrock layers at the peak of the dry season, the drought-deciduous *E. cyclocarpum* was extracting water from depths >1 m. Leaf flushing during the driest months of the year in *E. cyclocarpum* may require a more constant and reliable water source than *F. cotinifolia*, which may be able to modulate the timing of new leaf production according to water availability in the shallow soil. Jackson et al. (1999) and Stratton et al. (2000) found that drought-deciduous tree species tended to rely on deeper water sources than evergreen species in a Brazilian Cerrado savanna and in a Hawaiian dry tropical forest, respectively. An alternative explanation is that large water storage in succulent trunks or roots might have decoupled leaf flushing from seasonal water availability in some of the drought-deciduous tree species (Chapotin et al. 2006), which illustrates the numerous combinations of plant traits that can combine to produce different water use strategies in the same dry tropical ecosystem (Borchert et al. 2004).

The mean foliar $\delta^{13}C$ value for all the tree species investigated was $-27 \pm 0.5‰$. This value is 2–3‰ more enriched than those reported for other seasonally dry tropical forests elsewhere (Sobrado and Ehleringer 1997; Leffler and Enquist 2002). The evergreen species *B. alicastrum* had a mean leaf $\delta^{13}C$ value which was 1.9‰ less negative than that measured by Leffler and Enquist (2002) in a dry tropical forest in Costa Rica, which indicates that water stress is comparatively greater for trees growing on shallow karst soils in northern Yucatan (Stewart et al. 1995). $\delta^{13}C$ showed a 3.4‰ range of variation among tree species, suggesting a high degree of plant functional diversity possibly associated with differences in carbon assimilation and water use strategy (Martinelli et al. 1998). The evergreen species *B. alicastrum* and *T. olivaeformis* showed lower foliar $\delta^{13}C$ than any of the drought-deciduous species, which agrees with the pattern found by Sobrado and Ehleringer (1997) in a dry tropical forest in Venezuela, by Bonal et al. (2000) in a seasonal rainforest in Guiana or by Franco et al. (2005) in a Brazilian Cerrado savanna. Newly formed foliar tissue produced during the dry season was used for $\delta^{13}C$ analyses in drought-deciduous species, as all of them initiated leaf

flushing before the onset of the rainy season. Therefore the high foliar $\delta^{13}C$ values exhibited by *E. cyclocarpum*, *S. purpurea*, or *C. odorata* might indicate high water use efficiency in response to dry environmental conditions during leaf formation. By contrast, the leaf material used for $\delta^{13}C$ analyses in the evergreen species *B. alicastrum* and *T. olivaeformis* had been formed under wetter conditions, because these species only flush new leaves after the onset of the rainy season. Interestingly, the evergreen species *F cotinifolia* exhibited high $\delta^{13}C$ values within the range typical of drought deciduous trees, suggesting that the relationship between tree leaf phenology and foliar $\delta^{13}C$ is not straightforward in these agroecosystems. Aside from water use efficiency, other factors such as leaf age, leaf morphology or foliar nutrient concentration may have played a role in the observed differences in $\delta^{13}C$ among species (Dawson et al. 2002). For example, the high $\delta^{13}C$ values of *E. cyclocarpum* could be partly the result of high foliar N concentration in this N-fixing leguminous tree.

In conclusion, our data suggest that native trees growing on shallow karst soils in northern Yucatan depend mostly on water stored within the upper 2–3 m of the soil/bedrock profile even during the pronounced dry season. Groundwater was not the major source of water for any of the tree species investigated. The thick limestone shell overlying the aquifer appears to hamper root penetration down to the phreatic level, thus preventing heavy utilization of groundwater by the trees during drought. Despite the small water storage capacity of the thin soil, moisture content in subsurface soil-filled cavities and in the porous limestone bedrock is apparently enough to sustain even adult evergreen trees during the dry season. To our knowledge, this is the first isotopic study to address partitioning of water resources among native tree species in the Yucatan peninsula. Vertical partitioning of soil/bedrock water may decrease competition and promote tree species' coexistence in the dry tropical climate of the Yucatan peninsula, which is relevant to the design and management of mixed agroforestry systems and forest plantations. Considering that current empirical models predict some of the greatest rooting depths of any biome for seasonally dry tropical ecosystems (Schenk and Jackson 2002, 2005), these results have wider implications for water balance and hydrological cycle studies (Nepstad et al. 1994) in forested tropical karst regions.

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