

Utilization of bedrock water by *Brosimum alicastrum* trees growing on shallow soil atop limestone in a dry tropical climate

José Ignacio Querejeta ·
Héctor Estrada-Medina · Michael F. Allen ·
Juan J. Jiménez-Osornio · Rocío Ruenes

Received: 17 March 2006 / Accepted: 1 June 2006 / Published online: 24 August 2006
© Springer Science+Business Media B.V. 2006

Abstract Adult evergreen Ramón (*Brosimum alicastrum* Sw. Moraceae) trees can thrive on the shallow soils atop limestone of northern Yucatan despite limited soil water storage capacity, and do not require irrigation during the annual dry season. We hypothesized that early development of deep roots to reach moist subsoil layers or groundwater is critical to the performance of ramón trees growing on thin soils (~5 cm deep) over limestone bedrock. We conducted an isotopic study in a non-irrigated ramón plantation aimed at determining the sources of water used by trees of different age (5 or 9 years old) at the peak of the dry season. Pit excavation showed

that *Brosimum alicastrum* roots were mostly concentrated in the upper soil and bedrock layers. About 5-year-old trees showed a much sharper decrease in shoot water content (21%) than 9-year-old ones (10%) during the dry season. Foliar $\delta^{13}\text{C}$ values were significantly higher in 5-year-old trees ($-27.5 \pm 0.3\text{‰}$) than in 9-year-old ones ($-28.5 \pm 0.3\text{‰}$), indicating greater water use efficiency and water stress levels in the younger age group. The $\delta^{18}\text{O}$ signature of stem water did not differ significantly between tree age groups at either sampling date. Stem water $\delta^{18}\text{O}$ values of *Brosimum alicastrum* trees at the peak of drought ($-2.3 \pm 0.3/-2.9 \pm 0.3\text{‰}$) were significantly different from groundwater ($-4.3 \pm 0.1\text{‰}$) for both age groups. According to $\delta^{18}\text{O}$ data, ramón trees utilized bedrock water from depths between 0.5 and 2.5 m during the late dry season. Better dry-season water status in 9-year-old trees compared to 5-year-old ones appeared to be more the result of greater volume of soil and bedrock explored for water than the outcome of deeper rooting depth. The ability to take up water stored in the upper few meters of the weathered limestone bedrock during the pronounced dry season is likely the key feature allowing *Brosimum alicastrum* to thrive under non-irrigated conditions in the shallow, rocky soils of the Yucatan. Locally adapted native tree species capable of efficiently extracting water from bedrock may be the only perennial crops suitable for rainfed cultivation in

J. I. Querejeta · H. Estrada-Medina · M. F. Allen
Center for Conservation Biology, The University of
California, Riverside, CA 92521, USA

J. J. Jiménez-Osornio · R. Ruenes ·
H. Estrada-Medina
Departamento de Manejo y Conservación de
Recursos Naturales Tropicales (PROTROPICO),
Facultad de Medicina Veterinaria y Zootecnia,
Universidad Autónoma de Yucatán (FMVZ-UADY),
Mérida, Yucatán, México

J. I. Querejeta (✉)
Departamento de Conservación de Suelos y Aguas,
Centro de Edafología y Biología Aplicada del Segura-
Consejo Superior de Investigaciones Científicas
(CEBAS-CSIC), P.O. Box 4195, Campus de
Espinardo 30100, Murcia, Spain
e-mail: querejeta@cebas.csic.es

the shallow soils atop limestone of northern Yucatan.

Keywords Drought · Groundwater · Weathered limestone · Stable isotopes · $\delta^{13}\text{C}$ · $\delta^{18}\text{O}$

Introduction

Soils developed on weathered limestone bedrock in the Yucatan peninsula are shallow and rocky and typically have little moisture storage capacity (Duch 1995; Weidie 1985). Despite limited water storage, these soils can support woody vegetation with large standing biomass under the seasonally dry tropical climate of northern Yucatan. Large trees can be found in natural forests (Cairns et al. 2003) and homegardens (Jiménez-Osornio et al. 1999) throughout the region, indicating that shallow soil does not represent a major hindrance for the establishment and growth of native tree species. For this reason, agroforestry systems are considered a suitable alternative to slash and burn agriculture after abandonment of henequen (*Agave fourcroydes* Lem.) cultivation in many areas of the northern Yucatan Peninsula (Montañez-Escalante et al. 2005; Negreros-Castillo and De Clerck 1999).

The Ramón (*Brosimum alicastrum* Sw. Moraceae) is a native evergreen tree species which has traditionally been considered an important crop by the Maya people in the Yucatan, and is still widely cultivated in their homegardens (Gillespie et al. 2004; Peters and Pardo-Tejada 1982). *Brosimum alicastrum* trees produce large amounts of high quality fodder during the dry season, which has led to the establishment of ramón plantations dedicated to forage production for livestock since the 1970's (Ayala and Sandoval 1995). Adult *Brosimum alicastrum* trees can thrive on shallow soils atop limestone and do not require irrigation during the prolonged dry season of northern Yucatan, which suggests root access to subsoil moisture or groundwater (Gillespie et al. 2004). However ramón seedlings and saplings may require frequent watering to survive the dry season during the first few years after establishment (Gillespie et al., 2004). Several studies conducted in the greenhouse have shown that the

performance of ramón seedlings is very sensitive to water stress (Gillespie et al. 2004; Rasmussen 1990), but little is known about the water use strategy and moisture sources of *Brosimum alicastrum* trees growing on shallow soils under natural field conditions.

Jackson et al. (1999) suggested that rapid development of deep roots to reach soil layers where substantial water depletion does not occur may facilitate establishment and survival of young trees in seasonally dry tropical ecosystems. We hypothesized that early development of deep roots to reach moist subsoil layers or groundwater is critical to the performance of ramón trees growing on thin soil over limestone in the seasonally dry tropical climate of northern Yucatan. We further hypothesized that access to moist subsoil layers or groundwater buffers ramón trees from drought stress during the severe dry season, while saplings with shallower roots experience more severe water stress. In order to test these hypotheses, we conducted an isotopic study in a non-irrigated ramón plantation on shallow soil (about 5 cm deep) aimed at determining the sources of water used by trees of different age at the peak of the dry season.

The carbon stable isotope composition of plant tissues reflects the interplay among all aspects of plant carbon and water relations and can be used as an integrator of whole plant function (Dawson et al. 2002). In C3 plants, discrimination against ^{13}C versus ^{12}C by the Rubisco enzyme is linked to photosynthesis via c_i/c_a , the ratio of intercellular to ambient CO_2 concentrations (Farquhar et al. 1982). This ratio reflects the relative magnitudes of photosynthetic rate and stomatal conductance, so analyses of carbon stable isotopes at natural abundance in leaf tissue serve as a surrogate for estimating intrinsic water use efficiency (WUE, the ratio of carbon acquired to water vapour losses via stomatal conductance). Variation in leaf $\delta^{13}\text{C}$ is caused by genetic and environmental factors that influence gas exchange through morphological and functional plant responses. Environmental factors influencing leaf $\delta^{13}\text{C}$ include soil moisture, relative humidity, irradiance, temperature and nitrogen availability (Dawson et al. 2002). Generally plants with high $\delta^{13}\text{C}$ are thought to have high WUE. Drought

stress tends to enhance WUE because stomatal conductance is comparatively more strongly affected by water limitation than carbon assimilation, thus leading to increased leaf $\delta^{13}\text{C}$ values. Therefore leaf $\delta^{13}\text{C}$ measurements can help explore the range of variation in water use efficiency and drought stress levels among conspecific trees of different age (Dawson et al. 2002).

The zones of active water uptake by plant roots can be determined through analyses of oxygen stable isotope ratios at natural abundance, which allow discrimination among different potential moisture sources (Brunel et al. 1995; Ehleringer and Dawson 1992). There is no isotopic fractionation during water uptake by terrestrial plants, so the $\delta^{18}\text{O}$ of stem water reflects that of the source water (Dawson et al. 2002). In tropical regions the isotopic signature of rainfall water often exhibits little seasonal variation (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 isotope (^{18}O) due to evaporative fractionation, resulting in steep gradients in oxygen isotopic signatures with depth (Barnes and Turner 1998). Therefore the stem water isotopic signatures of deep and shallow rooted trees are expected to differ most widely at the peak of the dry season.

Materials and methods

Site description

The study was carried out in a non-irrigated ramón (*Brosimum alicastrum* Sw. Moraceae) plantation in northern Yucatan (Fig. 1: Kampepén, 089°39'10" W; 20°50'00" N) between October 2001 and April 2002. The tree stand included interspersed ramón trees of 5 and 9 years of age planted on a 3 × 3 m planting grid. Average trunk diameters of 9 and 5 year-old ramón trees were 15 ± 1.1 and 6.2 ± 0.9 cm, respectively. Height of 5-year-old trees was 1.8–3 m, while 9-year-old ones were 2.5–4.5 m high. Average annual temperature at this site is 27.2°C, and total annual precipitation is approximately 1,000 mm,

with a rainy season normally extending from May through October. The area experiences a pronounced 4–6 month dry season in the winter months during which only about 10–20% of the total annual rainfall is received (Orellana et al. 1999). The topography of Northern Yucatan is mostly flat, and the lithology consists of highly permeable Tertiary limestones and dolomites (Weidie 1985). Soils are extremely shallow and rocky (Duch 1995; Estrada-Medina 2000). Organic matter content is very high in these soils, ranging from 23.5% to 49.9% (Bautista-Zuñiga et al. 2004). Total soil nitrogen content is around $1.4 \pm 0.7\%$ (Campos and Dirzo 2003). 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 (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 1995; González-Herrera et al. 2002) is often found near the ground surface. Below the shallow soil and consolidated limestone layers there is a soft, squeezable, weathered limestone of high porosity (35–50% compared to 5–15% of consolidated limestone; Estrada-Medina et al. 2005), which is locally termed “sascab”. Subsurface sascab strata can be several meters thick. 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, with little (<1 m) interseasonal fluctuations (pers. obs.).

Sampling

Trees were sampled for oxygen stable isotope analysis in October 2001 (end of rainy season) and in April 2002 (peak of dry season). Eight trees per tree age group were sampled on both occasions. 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

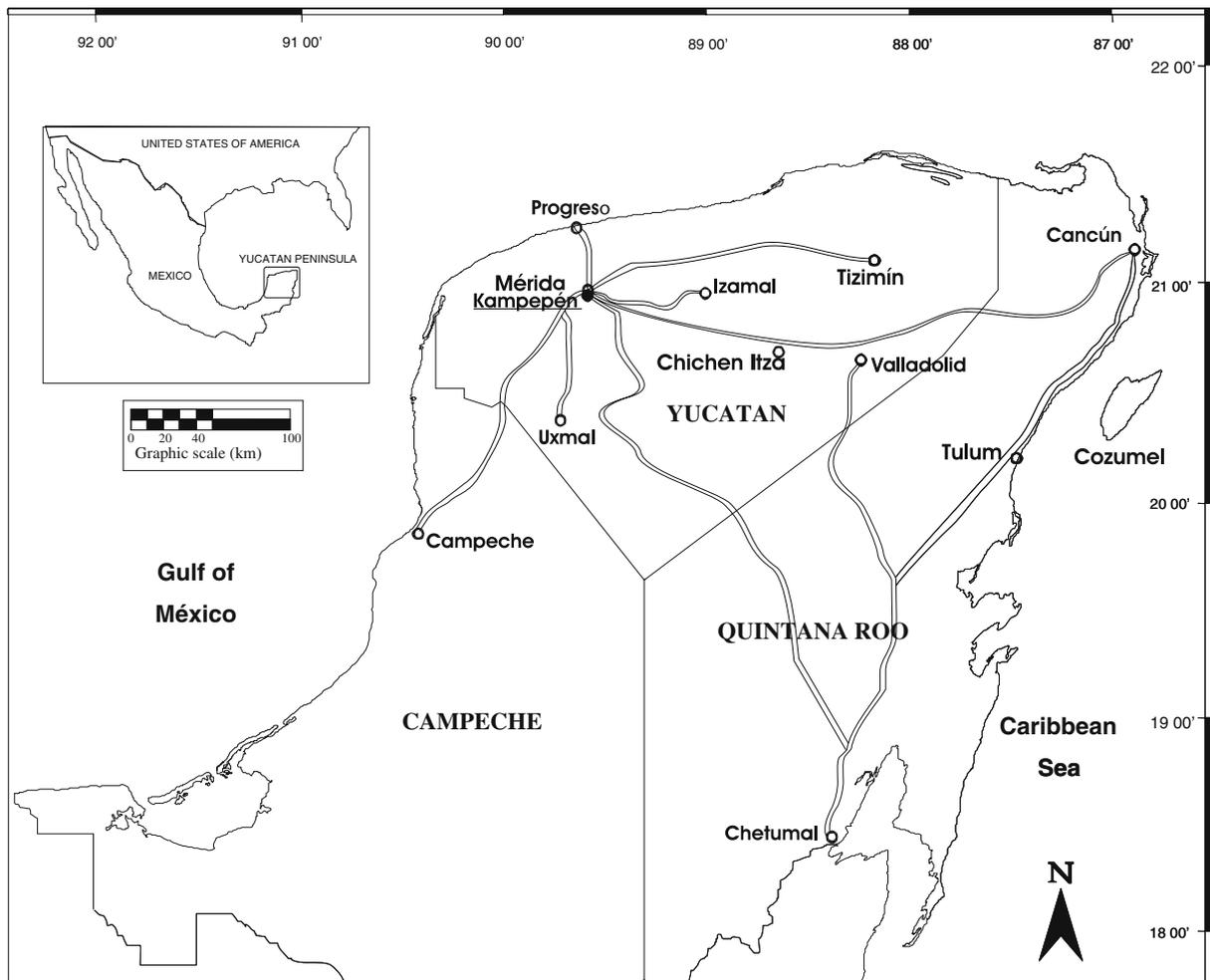


Fig. 1 Map of the Yucatan peninsula showing the location of the Kampepén experimental area

(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 for later processing and analysis.

Soil/bedrock samples were collected at the peak of drought in late April 2002. One pit 2 m in diameter was excavated amidst the *Brosimum alicastrum* trees included in the study to characterize all possible sources of water. The pit was manually excavated by a team of three local Maya well-drillers using picks, shovels and dynamite. The pit was dug down to a depth of 9 m until the groundwater table was reached. Due to budget constraints, we decided to excavate the pit at the time of the year when depth gradients in oxygen

isotopic signatures as well as vertical partitioning of water sources between tree age groups were more likely to occur. The extremely shallow and rocky soil at the experimental site precluded more extensive sampling of potential water sources. Soil/bedrock samples were promptly taken from freshly excavated pit sidewalls for water content measurement and for oxygen isotope analysis of water. For each depth, 3–5 replicate soil/bedrock samples were collected from the 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 oxygen isotope analyses. Groundwater samples were obtained from the bottom of the pit after the aquifer was reached.

Water was extracted from soil and plant stem samples using a cryogenic vacuum distillation line (Ehleringer et al. 2000). The water content of stems, soil and bedrock samples was calculated according to differences in sample weight before and after thorough water extraction (100°C, 3 h). Oxygen stable isotope analyses were conducted at the Centre for Stable Isotope Biogeochemistry of the University of California at Berkeley. $\delta^{18}\text{O}$ 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 ml m^{-3} or 3,000 ml m^{-3} CO_2 in He. After 48 h, CO_2 in the head space was analysed 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). $\delta^{18}\text{O}$ values are expressed in delta notation (‰) relative to an accepted international standard (V-SMOW) (Ehleringer and Dawson 1992). Analytical precision of $\delta^{18}\text{O}$ measurements was $\pm 0.18\text{‰}$.

In late April 2002, sunlit, mature leaf samples were collected from the same *Brosimum alicastrum* trees included in the water source determination study. All the sampled leaves had been formed during the rainy season prior to the study. Leaf material was oven dried, ground and analyzed for $\delta^{13}\text{C}$. Analyses were conducted on a continuous flow mass spectrometer (Europa Scientific Hydra 20/20, Chelshire, England) at the Stable Isotope Facility of the University of California at Davis. $\delta^{13}\text{C}$ 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 content values,

$\delta^{18}\text{O}$ data and leaf $\delta^{13}\text{C}$ data were subjected to the Student's *T* test in order to detect significant (<0.05) differences between the two tree age groups. Within each age group, stem water content values and $\delta^{18}\text{O}$ data were analysed by Student's *T* test to detect seasonal differences between sampling dates.

Results

At the end of the rainy season in October 2001, *Brosimum alicastrum* showed similar average stem water contents in the two tree age groups (Table 1). Stem water contents in ramón trees decreased significantly (Student's *T* test; $P < 0.001$) over the course of the dry season for both age groups. However 5-year-old trees showed a much sharper decrease in shoot water content (21%) than 9-year-old ones (10%) during the dry season (Table 1). The $\delta^{18}\text{O}$ signature of stem water did not differ significantly between tree age groups at either time of sampling (Student's *T* test; $P > 0.05$). In 9-year-old trees the $\delta^{18}\text{O}$ of stem water was significantly ($P < 0.05$) more enriched in May 2002 than in October 2001 (0.9‰ increase), suggesting utilization of water sources subject to progressively greater evaporative isotopic enrichment. By contrast, stem water $\delta^{18}\text{O}$ remained nearly unchanged between sampling dates in 5-year-old trees. Foliar $\delta^{13}\text{C}$ values were significantly higher in 5- than in 9-year-old trees at the peak of drought, indicating greater water use efficiency and water stress in the younger age group. Across age groups, foliar $\delta^{13}\text{C}$ in ramón trees correlated negatively ($r^2 = -0.626$; $P < 0.05$) with shoot water content (Fig. 2).

Table 1 Shoot water content determined by weight difference after water extraction, $\delta^{18}\text{O}$ of stem water, and leaf $\delta^{13}\text{C}$ in interspersed 5 and 9-year-old *Brosimum alicastrum* trees in a forest farm plantation in Kampepén

	Stem water content (%)		Stem water $\delta^{18}\text{O}$ (‰)		Foliar $\delta^{13}\text{C}$ (‰)
	October 2001	April 2002	October 2001	April 2002	April 2002
<i>Brosimum</i> 9-year-old ($n = 8$)	47.7 \pm 0.5	43 \pm 0.8**	-3.2 \pm 0.1	-2.3 \pm 0.3	-28.5 \pm 0.3*
<i>Brosimum</i> 5-year-old ($n = 8$)	46.5 \pm 0.8	36.9 \pm 0.6	-3 \pm 0.7	-3 \pm 0.7	-27.5 \pm 0.3

Stem water content and stem water $\delta^{18}\text{O}$ were measured at the end of the rainy season (October 2001) and at the peak of the dry season (April 2002), while foliar $\delta^{13}\text{C}$ was measured in April 2002 only. Means \pm standard errors are shown for all variables

*Values in same column significantly different at $P < 0.05$; **Significantly different at $P < 0.001$

Pit excavation in April 2002 exposed an extremely rocky, shallow soil 5 cm deep overlying heterogeneous fractured bedrock (Fig. 3). A very hard limestone layer (“laja”) near the ground surface was underlain by softer bedrock of high porosity (“sascab”). Some soil-filled cracks and crevices were encountered within the limestone bedrock matrix in the upper 200 cm of the profile. The soil was classified as Lithic Leptosol according to the FAO system. Although root density in the soil/bedrock profile was not quantified in this study, visual inspection of pit sidewalls suggested that *Brosimum alicastrum* roots were mostly concentrated in the upper soil and bedrock layers. Root density appeared to be very high in the thin topsoil layer as well as in soil pockets within the limestone bedrock matrix. Dense mats of roots were encountered growing along cracks in the bedrock. Sascab bedrock strata in the upper 200 cm of the profile were colonized by fine roots as well. Root abundance appeared to decline sharply with depth, and no roots could be found below 200 cm despite careful visual inspection of pit sidewalls.

Total rainfall during the twelve months prior to soil/bedrock sampling was 70% of the long term mean (702.6 mm) in the experimental area (Fig. 4). Only 9 mm of rain were recorded during March and April 2002. At the peak of drought in late April 2002, gravimetric water content in the

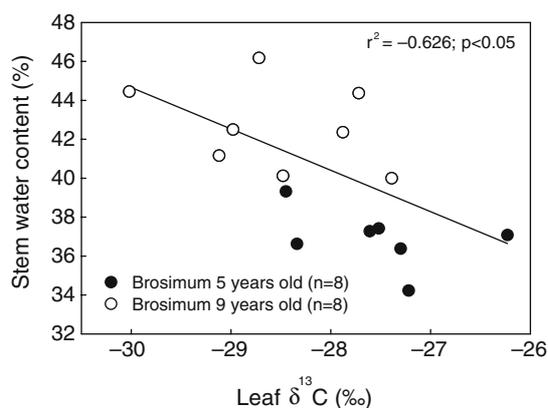


Fig. 2 Relationship between the carbon isotope composition of foliar tissue and stem water content in 5- and 9-year-old *Brosimum alicastrum* trees in a non-irrigated farm forest plantation in Kampepén. Samples were collected in late April 2002 at the peak of the dry season

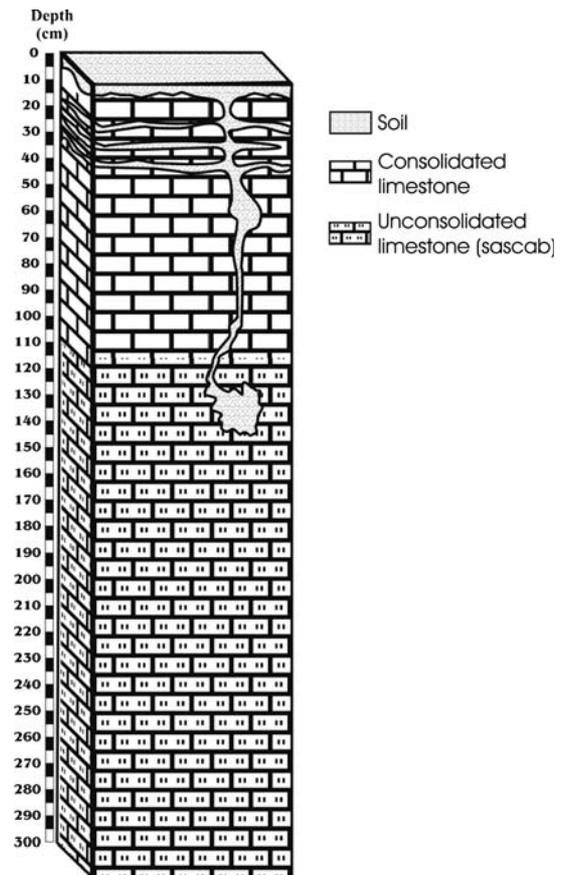
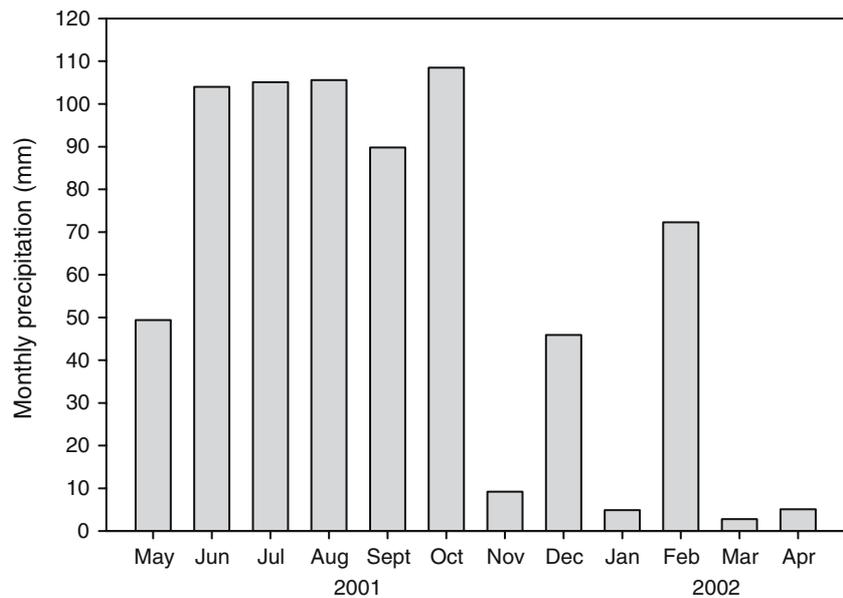


Fig. 3 Schematic of the upper 3 m of the soil/bedrock profile observed in the excavated pit, showing the distribution of cracks and of soil filled cavities in the limestone

upper 600 cm of the soil/bedrock profile fluctuated between 8% and 15%, and no clear trend with depth was observed (Fig. 5a). Mean soil/bedrock water content values showed large standard errors, reflecting an heterogeneous profile composed of soil pockets interspersed within an intricate matrix of limestone bedrock strata with varying water holding capacities. The markedly seasonal rainfall pattern in northern Yucatan favoured the development of a steep vertical isotopic gradient in the soil/bedrock profile during the dry season. Evaporative isotopic enrichment of soil/bedrock water was very pronounced near the surface but declined sharply with depth (Fig. 5b). The $\delta^{18}\text{O}$ signature of bedrock water closely approached that of aquifer water at around 300 cm depth. Groundwater samples

Fig. 4 Monthly rainfall distribution during the May 2001–April 2002 period at the experimental area



collected at the bottom of the experimental pit had an average $\delta^{18}\text{O}$ value of $-4.3 \pm 0.1\text{‰}$ ($n = 3$). According to $\delta^{18}\text{O}$ data, ramón trees of both age groups appeared to be utilizing bedrock water from depths between 50 cm and 250 cm during the late dry season (Fig. 5b). Stem water $\delta^{18}\text{O}$ values of ramón trees at the peak of drought were significantly different from groundwater for both age groups ($P < 0.001$; Mann–Whitney U -test).

Discussion

Large decreases in stem water content between October 2001 and April 2002 indicated that considerable water stress developed in ramón trees of both age groups during the dry season (Bradford and Hsiao 1982). These results suggest that groundwater was not the major source of water for ramón trees during the dry season, as phreatophytic species tapping a permanent water table are usually well buffered from seasonal drought (Gries et al. 2003; Zencich et al. 2002). The pattern of root distribution encountered in the pit at the Kampepén plantation supported this interpretation, as no roots could be found below 2 m depth despite careful visual inspection of pit sidewalls. Further, ramón trees had stem water

$\delta^{18}\text{O}$ values which departed significantly from the groundwater $\delta^{18}\text{O}$ signature. Stem water $\delta^{18}\text{O}$ values at the peak of the dry season were between 1.2‰ and 2‰ more enriched than aquifer water, depending on tree age group. 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 (Chimner and Cooper 2004; Ewe et al. 1999; Flanagan et al. 1992; Snyder and Williams 2000; Zencich et al. 2002). Groundwater utilization by woody vegetation under seasonally dry climates has been shown before to decrease with depth to the phreatic level, even when the strata overlying the aquifer are easier to penetrate by roots than limestone bedrock (Cramer et al. 1999; Farrington et al. 1996; Zencich et al. 2002).

According to $\delta^{18}\text{O}$ data, ramón trees of both age groups relied on water stored within the upper 2.5 m of the fractured limestone bedrock during the dry season. Total precipitation during the dry season (November 2001–April 2002) at Kampepén was 140 mm, which prevented complete depletion of moisture in the upper layers of the soil/bedrock profile (Fig 5a). Water stored in bedrock strata plays a critical role in supporting tree transpiration during dry periods in ecosystems with shallow soils (e.g., Hubbert et al. 2001;

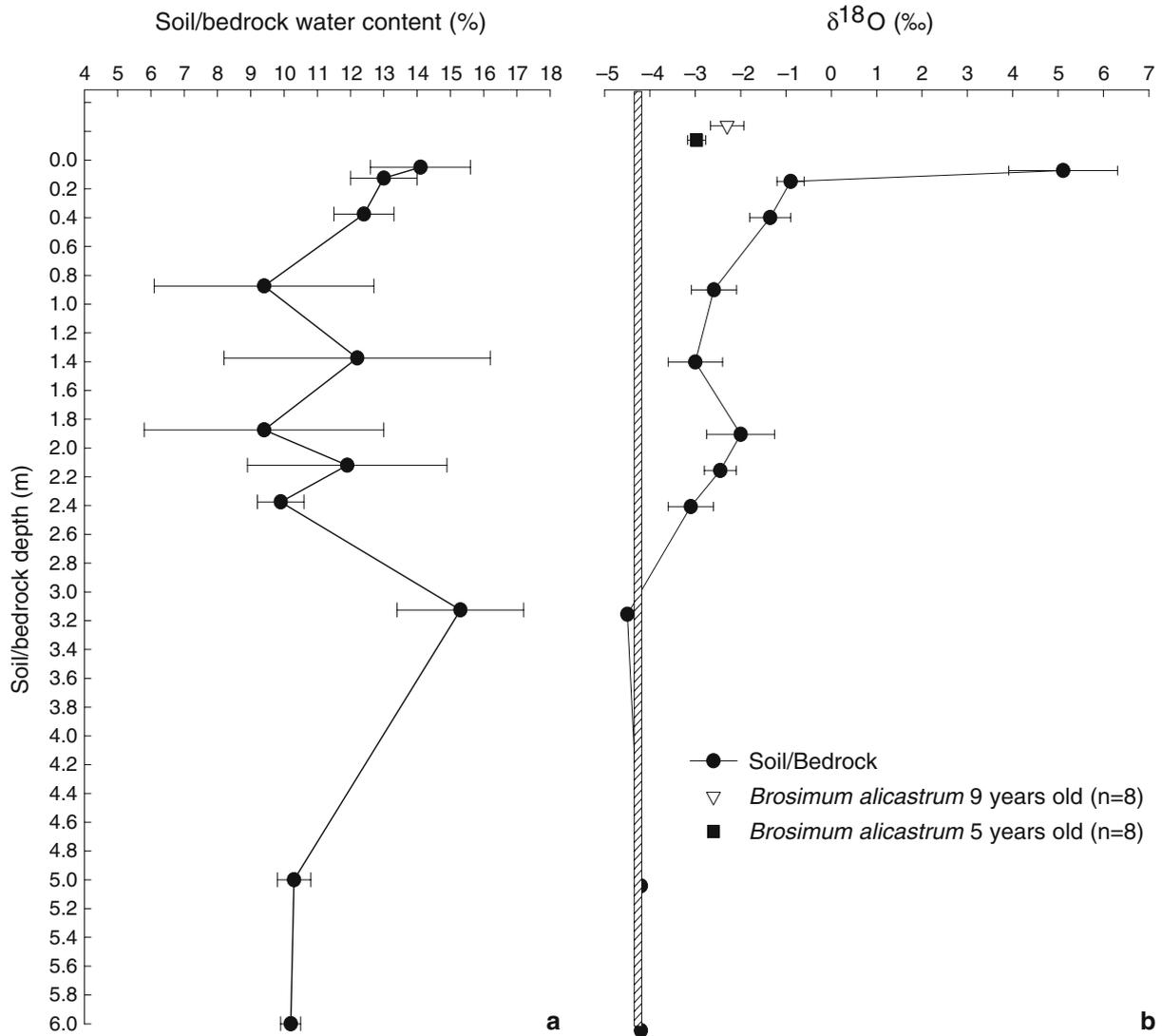


Fig. 5 Gravimetric water content and $\delta^{18}\text{O}$ of soil water in the soil/bedrock profile in Kampepén at the peak of the dry season in late April 2002. Figure 5a Soil/bedrock water contents. Values at each depth represent the average and standard error of 3–5 soil/bedrock samples collected from the sidewalls of a single pit excavated through the limestone bedrock using dynamite. Figure 5b. Average

$\delta^{18}\text{O}$ isotopic profile of soil/bedrock water and $\delta^{18}\text{O}$ values of stem water in *Brosimum alicastrum* trees. Values at each depth represent means and standard errors of three soil/bedrock samples collected from the sidewalls of the pit ($n = 3-5$). The crossed bar represents the $\delta^{18}\text{O}$ value of groundwater

Rose et al. 2003; Zwieniecki and Newton 1996). Weathered limestone bedrock can hold significant amounts of water (Fig 5a) that appears to be accessible to ramón roots, as indicated by the presence of fine roots in sascab bedrock strata. Macropores or preferred pathways for water percolation in the fractured limestone matrix likely contributed to the recharge of bedrock

during the wet season, and following occasional rain during the dry season. Downward transfer of excess water from topsoil to underlying limestone by tree roots after rain (reverse hydraulic lift, or hydraulic descent) may have also contributed to the rapid recharge of bedrock (Burgess et al. 2001). Water redistributed to deeper bedrock or to soil pockets within the limestone matrix would

be better protected from evaporation and shallow rooted competitors. Several studies conducted in seasonally dry tropical ecosystems elsewhere have also found that most tree species depend on water stored within the upper 1–4 m of the soil/bedrock profile during the dry season (Jackson et al. 1999; Sternberg et al. 2002; Stratton et al. 2000), even at sites where shallow (2–4 m) groundwater is available (Drake and Franks 2003).

Ramón trees in Kampepén had a mean leaf $\delta^{13}\text{C}$ value which was 2–3‰ less negative than that measured by Leffler and Enquist (2002) for the same species in a dry tropical forest in Costa Rica. This indicates that the thin, rocky soils in northern Yucatan impose a comparatively greater water stress on this evergreen tree species (Stewart et al. 1995). Whereas 9-year-old ramón trees showed lower foliar $\delta^{13}\text{C}$ values and a smaller dry-season decline in shoot water content than 5-year-old ones, stem water $\delta^{18}\text{O}$ signatures were not significantly different in the two age groups, which indicates similar water extraction depths at the peak of drought. According to $\delta^{18}\text{O}$ data, rooting depth of ramón trees in Kampepén was at least 0.8–1.4 m. However the $\delta^{18}\text{O}$ of stem water in ramón trees was also similar to that of bedrock water in the 1.8–2.5 m depth interval. Better dry-season water status in 9-year-old ramón trees (indicated by their significantly higher shoot water content in April) appeared to be the result of greater lateral root spread permitting exploration of a larger soil/bedrock volume compared to 5-year-old trees (Casper et al. 2003). Greater development of roots in 9-year-old trees may have also allowed more thorough exploitation of water stored in soil pockets within the bedrock matrix. Large inter-tree variabilities within tree age groups in stem water content, stem water $\delta^{18}\text{O}$ and foliar $\delta^{13}\text{C}$ suggested strong microsite effects on the water status of ramón individuals. Horizontally uneven thickness of the topsoil layer, irregular spatial distribution of subsurface soil pockets, or preferential infiltration of rainfall water along cracks in the limestone bedrock could have contributed to contrasting water availability among microsites at the Kampepén plantation.

In conclusion, ramón trees utilized water stored in the upper 2.5 m of the soil/bedrock

profile during the dry season. Contrary to initial expectations, we found no indication of groundwater utilization in this native evergreen tree species during the annual peak of drought. Although water stored in the bedrock was sufficient to sustain ramón trees throughout the dry season, trees experienced considerable water stress, as indicated by sharp decreases in stem water content. Better dry-season water status in bigger and older trees compared to younger and smaller ones appeared to be more the result of greater volume of soil explored for water than the outcome of deeper rooting depth. The ability to take up water stored in the upper few meters of the limestone bedrock during the pronounced dry season is likely the key feature allowing *Brosimum alicastrum* to thrive under non-irrigated conditions in the shallow, rocky soils of northern Yucatan. It is interesting to note that soil nitrogen availability is generally not limiting for tree growth in northern Yucatan due to the dominance of nitrogen-fixing leguminous species in the local vegetation (Campo and Dirzo 2003). Our results suggest that locally adapted native tree species capable of efficiently extracting water from bedrock strata may be the only perennial crops suitable for rainfed cultivation in shallow rocky soils under seasonally dry tropical climate. Other co-occurring native tree crops frequently found in non-irrigated homegardens in the Yucatan (such as *Cordia dodecandra*, *Spondias purpurea* or *Talisia olivaeformis*) might also rely on bedrock water during the dry season.

Acknowledgements We thank David Magaña for allowing us to conduct this research in his Kampepén plantation. We also thank Angela López, Season Snyder and Roberto Lepe for their help with laboratory and field work. This research was supported by a UC MEXUS-CONACYT grant awarded jointly by the University of California Institute for Mexico and the United States, and the Mexican Comisión Nacional de Ciencia y Tecnología. We also thank the financial support of the American Institute for Global Change Research (IAI Project: Biogeochemical cycles under land use change in the semiarid Americas). JI Querejeta acknowledges a postdoctoral Fulbright Fellowship from the Spanish Ministerio de Educación y Ciencia, as well as financial support by the Biocomplexity Program (DEB 9981548) of the US National Science Foundation. Finally, we acknowledge the constructive comments of three anonymous reviewers.

References

- Ayala A, Sandoval SM (1995) Establecimiento y producción temprana de forraje de ramón (*Brosimum ali-castrum* Swartz) en plantaciones a altas densidades en el norte de Yucatán, México. *Agroforestería en las Américas* 7:10–16
- Barnes CJ, Turner JV (1998) Isotopic exchange in soil water. In: Kendall C, McDonnell JJ (eds) *Isotope tracers in catchment hydrology*. Elsevier, Amsterdam
- Bautista-Zuñiga F, Estrada-Medina H, Jiménez-Orsorio JJ, González-Iturbe JA (2004) Relación entre el relieve y unidades de suelo en zonas cársticas de Yucatán. *Terra Latinoamericana* 22:243–254
- Bradford KJ, Hsiao TC (1982) Physiological responses to moderate water stress. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) *Physiological Plant Ecology II. Water relations and carbon assimilation*. Encyclopaedia of Plant Physiology (New Series) vol 12B. Springer-Verlag, Berlin
- Brunel JP, Walker GR, Kenneth-Smith AK (1995) Field validation of isotopic procedures for determining sources of water used by plants in a semiarid environment. *J Hydrol* 167:351–368
- Burgess SO, Adams MA, Turner NC, White DA, Ong CK (2001) Tree roots: conduits for deep recharge of soil water. *Oecologia* 126:158–165
- Cairns MA, Olmsted I, Granados J, Argaez J (2003) Composition and aboveground tree biomass of a dry semi-evergreen forest on Mexico's Yucatan Peninsula. *For Ecol Manage* 186:125–132
- Campo J, Dirzo R (2003) Leaf quality and herbivory responses to soil nutrient addition in secondary tropical dry forest of Yucatan, Mexico. *J Trop Ecol* 19:525–530
- Casper BB, Schenk HJ, Jackson RB (2003) Defining a plant's belowground zone of influence. *Ecology* 84:2313–2321
- Chimner RA, Cooper DJ (2004) Using stable oxygen isotopes to quantify the water source used for transpiration by native shrubs in the San Luis Valley, Colorado USA *Plant Soil* 260:225–236
- Cramer VA, Thorburn PJ, Fraser GW (1999) Transpiration and groundwater uptake from farm forest plots of *Casuarina glauca* and *Eucalyptus camaldulensis* in saline areas of southeast Queensland, Australia. *Agric Water Manage* 39:187–204
- Dawson TE, Mambelli S, Plamboeck AH, Templer PH, Tu KP (2002) Stable Isotopes in Plant Ecology. *Annu Rev Ecol Syst* 33:507–559
- Drake PL, Franks PJ (2003) Water resource partitioning, stem xylem hydraulic properties, and plant water use strategies in a seasonally dry riparian tropical rainforest. *Oecologia* 137:321–329
- Duch GJ (1995) Los suelos, la agricultura y vegetación en Yucatán. In: Hernández E, Bello E, Levy S (eds) *La milpa en Yucatán: Un sistema de producción agrícola tradicional*. Colegio de Postgraduados, México
- Ehleringer JR, Dawson TE (1992) Water uptake by plants: perspectives from stable isotope composition. *Plant Cell Environ* 15:1073–1082
- Ehleringer JR, Roden J, Dawson TE (2000) Assessing ecosystem-level water relations through stable isotope analyses. In: Sala OE, Jackson RB, Mooney HA, Howarth RW (eds) *Methods in ecosystem science*. Springer, Berlin-Heidelberg-New York, pp 181–198
- Estrada-Medina H (2000) Caracterización y cartografía del recurso suelo del municipio de Hocabá, Yucatán. Tesis de Maestría en Manejo y Conservación de Recursos Naturales Tropicales. Mérida, Yucatán, México
- Estrada-Medina H, Graham RC, Allen MF, Jimenez-Orsorio JJM (2005) Karstic Features and Tree Root Development in Yucatán, México. ASA-CSSA-SSSA International Annual Meeting, Nov 6–10: Salt Lake City
- Ewe SML, Sternberg L, Busch DE (1999) Water use patterns of woody species in pineland and hammock communities of South Florida. *For Ecol Manage* 118:139–148
- Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and intercellular carbon dioxide concentration in leaves. *Aust J Plant Physiol* 9:121–137
- Farrington P, Turner JV, Gailitis V (1996) Tracing water uptake by jarrah (*Eucalyptus marginata*) trees using natural abundances of deuterium. *Trees* 11:9–15
- Flanagan LB, Ehleringer JR, Marshall JD (1992) Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. *Plant Cell Environ* 15:831–836
- Gillespie AR, Bocanegra-Ferguson DM, Jiménez-Orsorio JJ (2004) The propagation of Ramón (*Brosimum ali-castrum* Sw.; Moraceae) in Mayan homegardens of the Yucatan Peninsula of Mexico. *New Forests* 27:25–38
- González-Herrera R, Sánchez-Pinto I, Gamboa-Vargas J (2002) Groundwater flow modeling in the Yucatán karstic aquifer, México. *Hydrogeol J* 10:539–552
- Gries D, Zeng F, Foetzi A, Arndt SK, Bruelheide H, Thomas FM, Zhang X, Runge M (2003) Growth and water relations of *Tamarix ramosissima* and *Populus euphratica* on Taklamakan desert dunes in relation to depth to a permanent water table. *Plant Cell Environ* 26:725–736
- Hubbert KR, Beyers JL, Graham RC (2001) Roles of weathered bedrock and soil in seasonal water relations of *Pinus jeffreyi* and *Arctostaphylos patula*. *Can J For Res* 31:1947–1957
- Jackson PC, Meinzer FC, Bustamante M, Goldstein G, Franco A, Rundel PW, Caldas L, Iglar E, Causin F (1999) Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem. *Tree Physiol* 19:717–724
- Jiménez-Orsorio JJ, Ruenes-Morales MR, Montañés-Escalante P (1999) Agrodiversidad de los solares de la península de Yucatán. *Red, Gestión de Recursos Naturales* 14:30–40
- Leffler JA, Enquist BJ (2002) Carbon isotope composition of tree leaves from Guanacaste, Costa Rica: comparison across tropical forests and tree life history. *J Trop Ecol* 18:151–159

- Montañez-Escalante P, García-Barrios L, Jiménez-Osornio J (2005) Quarry reclamation in Mérida, Yucatán, México: a review on achievements and current limitations. *Trop Subtrop Agroecosyst* 5:101–108
- Negreros-Castillo P, De Clerck FA J (1999) Establecimiento de sistemas agroforestales multiestrato. *Red Gestión de Recursos Naturales* 14:18–21
- Orellana R, Balam-Ku M, Bañuelos-Robles I, García E, González-Iturbe JA, Herrera-Cetina F, Vidal-López J (1999) Evaluación climática. In: García de Fuentes A, Córdoba y Ordóñez J, Chico Ponce de León P (eds) Atlas de Procesos Territoriales de Yucatán. Universidad Autónoma de Yucatán, Mérida, pp 163–182
- Peters CM, Pardo-Tejada E (1982) *Brosimum alicastrum* (Moraceae) uses and potential in Mexico. *Econ Bot* 36:166–175
- Rasmussen YD (1990) The effects of light and water stress on *Brosimum alicastrum* seedlings. Master Sci. Thesis. University of California, Riverside
- Rose KL, Graham RC, Parker DR (2003) Water source utilization by *Pinus jeffreyi* and *Actostaphylos patula* on thin soils over bedrock. *Oecologia* 134:46–54
- Snyder KA, Williams DG (2000) Water sources used by riparian trees varies among stream types on the San Pedro River, Arizona. *Agric For Meteorol* 105:227–240
- Sternberg LD L, Moreira MZ, Nepstad DC (2002) Uptake of water by lateral roots of small trees in an Amazonian Tropical Forest. *Plant Soil* 238:151–158
- Stewart GR, Turnbull MH, Schmidt S, Erskine PD (1995) C-13 natural abundance in plant communities along a rainfall gradient: a biological integrator of water availability. *Aust J Plant Physiol* 22:51–55
- Stratton LC, Goldstein G, Meinzer FC (2000) Temporal and spatial partitioning of water resources among eight woody species in a Hawaiian dry forest. *Oecologia* 124:309–317
- Tu KP, Brooks PD, Dawson TE (2001) Using septum-capped vials with continuous-flow isotope ratio mass spectrometric analysis of atmospheric CO₂ for Keeling plot applications. *Rapid Comm Mass Spectrom* 15:952–956
- Weidie AE (1985) Geology of the Yucatan Platform. In: Ward WC (ed) Geology and hydrogeology of the Yucatan, Quaternary geology of northeastern Yucatan Peninsula. NOGS Publications, pp 1–19
- Weisbach C, Tiessen H, Jiménez-Osornio JJ (2002) Soil fertility during shifting cultivation in the tropical karst soils of Yucatan. *Agronomie* 22:253–263
- Yurtsever Y, Gat JR (1981) Atmospheric waters. In: JR Gat, Gonfiantini R (eds) Stable isotope hydrology: deuterium and oxygen-18 in the water cycle. International Atomic Energy Agency, Vienna, pp 103–142
- Zencich SJ, Froend RH, Turner JV, Gailitis V (2002) Influence of groundwater depth on the seasonal sources of water accessed by *Banksia* tree species on a shallow, sandy coastal aquifer. *Oecologia* 131:8–19
- Zwieniecki MA, Newton M (1996) Seasonal pattern of water depletion from soil-rock profiles in a Mediterranean climate in southwestern Oregon. *Can J For Res* 26:1346–1352