

Source water, phenology and growth of two tropical dry forest tree species growing on shallow karst soils

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Received: 6 September 2012 / Revised: 28 March 2013 / Accepted: 5 April 2013 / Published online: 13 April 2013
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Abstract Seasonally dry tropical forests are dominated by deciduous and evergreen tree species with a wide range of leaf phenology. We hypothesized that *Piscidia piscipula* is able to extend leaf senescence until later in the dry season due to deeper and more reliable water sources than *Gymnopodium floribundum*, which loses leaves earlier in the dry season. Physiological performance was assessed as timing of leaf production and loss, growth, leaf water potential, depth of water uptake determined by stable isotopes, and leaf stable isotopic composition of carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$). *P. piscipula* took water primarily from shallow sources, whereas *G. floribundum* took water from shallow and deep sources. The greatest variation in water sources

occurred during the onset of the dry season, when *G. floribundum* was shedding old leaves and growing new leaves, but *P. piscipula* maintained its leaves from the previous wet season. *P. piscipula* showed greater relative growth rate, greater leaf expansion rates, and more negative predawn and midday water potentials than *G. floribundum*. *P. piscipula* also exhibited greater leaf organic $\delta^{13}\text{C}$ and lower $\delta^{18}\text{O}$ values, indicating that the decrease in photosynthetic carbon isotope discrimination was associated with greater stomatal conductance and greater photosynthesis. Our results indicate that the contrasting early and late dry season leaf loss phenology of these two species is not simply determined by rooting depth, but rather a more complicated suite of characteristics based on opportunistic use of dynamic water sources, maximizing carbon gain, and maintenance of water potential during the dry season.

Communicated by M. A. Zwieniecki.

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Keywords Ground water · Yucatan · Rooting depth ·
Seasonally dry tropical forest · Stable isotopes

Introduction

Seasonally dry tropical forests are dominated by deciduous species coexisting with a small number of evergreen species (Holbrook et al. 1995). Trees withstand the dry season through two mechanisms of drought resistance: desiccation delay and desiccation tolerance (Tyree et al. 2003). Two important traits related to desiccation delay are leaf shedding (Eamus 1999) which reduces water loss, and depth of rooting (Tyree et al. 2002), which determines the sources of water and nutrients used by vegetation (Ehleringer and Dawson 1992; McCulley et al. 2004). Although previous reports suggested that evergreen species access relatively deeper water sources than deciduous species (Jackson et al. 1995),

more recent reports suggest that access to water is more related to tree size than phenology (Meinzer et al. 1999). However, there is relatively little information regarding differences among deciduous species having different timing or leaf shedding behavior, even though it is well known that leaf senescence behavior varies greatly among tropical dry forest tree species. Flushing and leaf abscission result from complex interactions between plants and their environment; in many species, the main abiotic factors driving these processes are solar radiation, air relative humidity, vapor pressure deficit, precipitation and soil water content (Lobo et al. 2003; Do et al. 2005; Zalamea 2008). Four main categories of leaf shedding phenology have been proposed by Williams et al. (1997): (1) evergreen species, which retain a full canopy throughout the year; (2) partially deciduous species, which lose up to 50 % of their canopy during the dry season; (3) semi-deciduous species, which lose more than 50 % of their canopy during the dry season; and (4) deciduous species, in which all leaves are lost during the dry season as they remain leafless for at least 1 month. Most tropical dry forest species are thought to deploy the majority of their root systems relatively deep in the soil profile where moisture tends to be greater and of longer duration (Holbrook et al. 1995). However, in northern Yucatan the hard upper limestone layer, beginning immediately below the shallow soil, impedes root growth, limiting downward growth to crevices and rhizoliths, and the occasional cavities filled with soil material (soil pockets) (Estrada-Medina et al. 2013). Rock crevices allow roots to grow far deeper than they would in unfractured bedrock (McMahon and Christy 2000). Thus, in the seasonally dry tropical forests of northern Yucatan, the ability of tree species to grow deep roots and access additional sources of water beyond topsoil could be a crucial characteristic related to variation in phenology and the relative abundance of contrasting tree species.

Sources of water used by trees can often be identified by comparing the isotopic composition of water from stems with potential water sources, because there is usually no isotopic fractionation of either hydrogen or oxygen isotopes during water uptake (Ehleringer and Dawson 1992). When trees take water from more than one source, the proportion of water absorbed from each source can be calculated using isotope mixing models (Phillips and Gregg 2003; Phillips et al. 2005). Such models were developed to cope with multiple sources and allow the input of ancillary data that are known about the system to constrain model outputs, thereby providing results that are restricted to real possibilities. Sources of water used by native trees in northern Yucatan have been studied using these approaches, and large variation in the depth of water uptake among deciduous and evergreen species has been observed (Querejeta et al. 2006, 2007). Furthermore, using these same isotopic approaches along a forest age chronosequence in northeastern Yucatan,

evergreen trees were found to access deeper water sources than deciduous species in early succession (Hasselquist et al. 2010). Thus, integrating rooting depth as a component of tropical dry forest tree strategies appears especially promising in complex karstic Yucatecan soils.

Water-use efficiency (WUE), the ratio of carbon gained in photosynthesis relative to water loss during transpiration (Lambers et al. 1998), is another key factor when considering the costs and benefits of a deep rooting system. Leaf carbon isotopic composition ($\delta^{13}\text{C}$) can be used to assess WUE in certain circumstances, and is often positively related to WUE because a high photosynthetic rate per unit stomatal conductance is usually associated with relatively low internal CO_2 concentration and reduces discrimination against $^{13}\text{CO}_2$ by rubisco (Farquhar et al. 1989). Although $\delta^{13}\text{C}$ has been used alone to infer WUE, its combination with analysis of isotopic composition leaf organic oxygen ($\delta^{18}\text{O}$) improves interpretation of leaf $\delta^{13}\text{C}$ values by allowing analysis of whether variation in $\delta^{13}\text{C}$ is due to changes on the photosynthetic activity or stomatal activity (Scheidegger et al. 2000; Barbour 2007). When humidity increases, the isotopic enrichment of leaf water decreases, causing a reduction in $\delta^{18}\text{O}$ (Roden and Ehleringer 1999). Theory and empirical data also demonstrate that $\delta^{18}\text{O}$ correlated negatively with stomatal conductance (Barbour et al. 2000). In shallow soils of northern Yucatan, Querejeta et al. (2006) showed that individuals of the same tree species differing in age had different WUE, with younger trees having greater WUE than older ones, indicating that these techniques hold promise for integrating potential differences in water sources with leaf physiological activity.

This study focuses on phenological variation between two dominant tropical dry forest species in relation to the depth of water uptake. We hypothesize that the late deciduous habit in *P. piscipula* and the early deciduous habit in *G. floribundum* may be determined by their ability to take water from different sources. *P. piscipula* may have access to deeper sources than *G. floribundum*. However, due to the restrictions for root growth imposed by the hard bedrock, both species will likely extract most of their water from shallow sources. We also hypothesize that differential use of water sources is linked to key ecophysiological measures of plant performance, including the timing of leaf fall, leaf size, leaf water potential and the balance of carbon gain and water loss as interpreted by leaf stable isotopic composition.

Materials and methods

Study site

This study was conducted in a limestone quarry located approximately 6 km south of Merida in the state of

Yucatán, México (20°54'18.86"N and 89°37'49.64"W). Altitude is 11 m above sea level, mean annual temperature is 25.2 °C, mean annual precipitation is 923.9 mm and mean relative humidity is 70 % (CONAGUA 2000). The wet season extends from June to October, and the dry season from November to May (Standley 1930; Orellana et al. 1999). Within these two main seasons, a cold front season occurs from September to March and hurricanes may occur from June to November.

Vegetation was a 15-year-old seasonally dry forest, aged based on accounts of workers at the quarry. The quarry is currently mined for gravel, lime and cement (Montañez-Escalante 2005). During quarry operations, vegetation and soil are removed several days before blasting of the rock to unearth vertical walls of approximately 7–8 m in height, exposing a completely new soil/bedrock profile almost every day (Fig. 1). Exposed walls extend from the land surface, down to just above the water table which lies at approximately 9 m depth. The soil/bedrock profile consists of a thin (0.1–0.3 m deep) layer of soil, three calcium carbonate rock layers (*laja*, *sascab* and *coquina*) and a variable number of scattered empty and soil filled cavities (soil pockets) (Table 1).

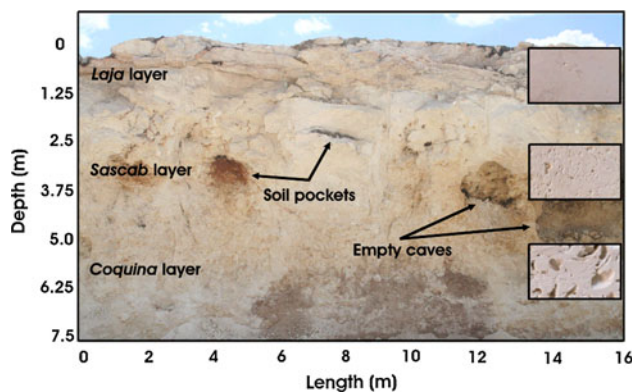


Fig. 1 Rock wall at the quarry site showing the three rock layers (*laja*, *sascab* and *coquina*). Close-ups are from the most abundant rock type in each layer

Study species

Water sources used by *Gymnopodium floribundum* (L.) Sarg (Maya name: Ts'i'ts'ilche) and *Piscidia piscipula* Rolfe (Maya name: Jabín) growing on shallow karst soils were identified and the performance of each species was monitored during 1 year. *G. floribundum* is an important tree species in the early successional stages of northern Yucatan forest (González-Iturbe et al. 2002), and its floral nectar is highly appreciated for apiculture purposes (Chemás and Rico-Gray 1991). *Piscidia piscipula* has more importance in the advanced successional stages of the forest and is used locally as timber, fuel and building material (Rico-Gray et al. 1991). *G. floribundum* and *P. piscipula* have noticeable morphological differences that could play into their strategies to overcome the dry season. *P. piscipula* is a faster growing tree with thicker bark and, thicker and larger leaves than *G. floribundum* (Standley 1930; Standley and Steyermark 1946; Ortiz 1994). Although both species are deciduous, *P. piscipula* has been reported as late deciduous because its leaf shedding starts later than other deciduous species (Nelson 1994).

Water sources and stem water

Water sources used by trees were evaluated using stable isotope analysis (Ehleringer and Dawson 1992; Allison et al. 1983). Topsoil, calcium carbonate rock layers, soil pockets and plant tissue samples were collected in three sampling campaigns: October 2007 (wet season), January 2008 (frontal season) and May 2008 (dry season).

Topsoil, bedrock and soil pocket samples were obtained from recently exposed walls. Sampling of the lower portion of the walls was restricted by the rock materials produced during blasting events, moreover, roots were not often observed growing in this layer; thus, soil pockets and rock samples were taken only from 0 to 5 m depth. Because topsoil was removed before rock blasting, soil samples were taken from areas up to 40 m away from the wall being sampled. In addition, gravimetric water content was evaluated by taking 20 samples from topsoil and each rock layer, and a variable number of samples from soil pockets depending on presence

Table 1 Characterization of vadose zone in northern Yucatán, México

Layer	Thickness (m)	Description	AWC (m ⁻³ m ⁻³)	PWS (m ³ ha ⁻¹)
Topsoil	0.3	Red soil, clay content ≈20 %	0.12	189
<i>Laja</i> layer	2.5	Consolidated hard rock	0.014–0.030	305–655
<i>Sascab</i> layer	2.5	Non-indurated soft rock	0.054–0.074	1,154–1,582
<i>Coquina</i> layer	4	Highly fossiliferous hard rock	0.011–0.025	431–980
Soil pockets	–	Scattered soil cavities filled with red soil, clay content ≈60 %	0.1107	718

Source of information: Estrada-Medina et al. (2010, 2013)

AWC Available water content, PWS potential water storage

of these features in the wall being sampled (normally 3–7) and drying at 105 °C. The eight water sources considered go down from the upper soil layer down to the ground water (topsoil 0–15 cm, topsoil 15–30 cm, *laja* 0–125 cm, *laja* 125–250 cm, *sascab* 250–375 cm, *sascab* 375–500 cm, soil pockets, and ground water).

Non-transpiring woody shoots were collected from five individuals of each species from vegetation within the quarry. Four stem samples of 5–10 mm width and 50–80 mm long were obtained from each tree. The same trees were sampled at each sampling campaign. No leaves or green tissue were included in the sample to avoid contamination of xylem water by isotopically enriched water that had undergone evaporation from the plant (Ehleringer and Dawson 1992). Samples were preserved in hermetic capped vials wrapped with parafilm and stored in the freezer until processed. Groundwater samples were taken from an open well 2 km from the quarry.

Water was extracted from topsoil, soil from pockets, rock and plant stem samples using a cryogenic vacuum distillation line (Ehleringer et al. 2000) for at least 60 min for stems and 40 min for soil and rocks (West et al. 2006). Water content of soil, bedrock and tree stems was calculated from subsamples taken right before the water extraction and oven dried for 24 h at 80 °C (stems) and 105 °C (soil and rock). Stable isotopic composition of oxygen ($\delta^{18}\text{O}$) and hydrogen ($\delta^2\text{H}$) analyses were conducted at the Centre for Stable Isotope Biogeochemistry at the University of California, Berkeley using a chromium-reactor interfaced with a continuous flow isotope ratio mass spectrometer (Delta Plus XL, Finnigan MAT GmbH, Germany). $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values were reported in delta notation (‰) relative to the Vienna Standard Mean Ocean Water (V-SMOW). Values of substrate and stem water $\delta^{18}\text{O}$ and $\delta^2\text{H}$ were plotted in a bi-variate relationship with the Meteoric Water Line determined for this region by Socki et al. (2002), to evaluate the role of water sources across seasons.

The contribution to tree water uptake from the different sources during the three sampling campaigns was calculated using Iso-Source software (Phillips and Gregg 2003). This software calculates ranges of source-proportional contributions to a mixture based on the isotopic signatures of the mixture and each of the sources. Both $\delta^{18}\text{O}$ and $\delta^2\text{H}$ data were used for model calculations. The data set for modeling was grouped as follows: (1) *Laja* 0–200 cm was disregarded because is not a significant source of water at any time (gravimetric water content; $\theta_g < 5\%$), (2) February data were not analyzed to avoid misinterpretations due to unsampled water sources (precipitation), (3) ground water was taken out of the analyses because root systems of *P. piscipula* and *G. floribundum* were not observed growing beyond 5-m depths and, (4) bedrock from 200–400 cm

was grouped as a single source because their isotopic values were very similar. Because sampled trees were growing <1 km from where rock samples were taken, we assumed that the isotopic compositions of rock were similar in both places. Results were reported as ranges of the most feasible contributions for each layer.

Growth, phenology and leaf measurements

Five individuals of *P. piscipula* and *G. floribundum* growing in a 40 × 40 m plot were monitored from June 2008 to May 2009. Growth was measured as the change in diameter at breast height (DBH) with a measuring tape, or height measured with a telescopic measuring rod, and expressed as relative growth rate (RGR). RGR was calculated as $(\ln X_2 - \ln X_1)/(t_2 - t_1)$, where $\ln X_2$ and $\ln X_1$ are the averages of the logarithmic transformed growth variable (RGR_{Height} or RGR_{DBH}) at the end (t_2) and the beginning (t_1) of the study (Hoffmann and Poorter 2002). Crown projected area was measured in two directions with a measuring tape. Leaf size was measured monthly on 20 mature leaves, randomly sampled from the middle part of each tree with a CI-202 Portable Area Meter (CID Bioscience, Inc. WA, USA). Leaves were then dried at 80 °C for 48 h and ground to a fine powder with a ball mill (8000D; Spex Sample Prep, Stanmore, UK) to assess stable isotope composition of carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$). Analysis of $\delta^{13}\text{C}$ was conducted at the Center for Stable Isotope Biogeochemistry at the University of California, Berkeley, using a PDZ Europa 20/20 isotope ratio mass spectrometer (Manchester, UK), and reported in delta notation (‰) relative to PDB (Pee Dee Belemnite) standard. Analysis of $\delta^{18}\text{O}$ was conducted at the University of California, Davis Stable Isotope Facility as CO in a High Temperature Conversion/Elemental Analyzer system (Thermo Fisher Scientific, Germany) interfaced with a continuous flow IRMS Europa Scientific Hydra (20/20) (Sercon Ltd., Cheshire, United Kingdom) and reported in delta notation (‰) relative to V-SMOW.

Monthly litterfall was sampled with one circular trap, 75 cm in diameter, located under the crown of each of the five measurement trees. Leaf water potential was measured at predawn (Ψ_{PD}) and midday (Ψ_{MD}) concurrent with wet, frontal and dry season water source measurements. Five mature leaves from the middle part of the canopy were cut per measurement tree and during each campaign. Water potential was assessed with a Scholander pressure chamber (model 670, PMS Instrument Company, OR, USA).

Statistical analysis

Variation between species in leaf size, litterfall and water potential was evaluated with an analysis of variance

(ANOVA). Variation between species in RGR_{Height} and RGR_{DBH} was evaluated using a two-tailed Student's t test. All statistical analyses were conducted in Prism (GraphPad Software Inc., La Jolla, CA, USA).

Results

Water sources and stem water

Gravimetric water contents (θ_g) of topsoil in the wet and frontal seasons were similar and three times greater than values measured in the dry season (Fig. 2). In rock layers, there were no differences in θ_g from 0 to 200 cm in depth during any season. In the dry season, the 200–500 cm part of the rock profile had a θ_g between 1 and 5 % but most values were under 1 %. Overall, soil pockets had the greatest θ_g ranging from 11 to 28 %. The θ_g of soil pockets was greater than that of topsoil during the dry season but lower during February and October. Stem water content in *P. pispicula* was greater than in *G. floribundum*. Average stem water contents measured in October, February and the dry season were 41, 45, and 37 % for *G. floribundum* and 56, 54, and 54 % for *P. pispicula*.

In the wet season, $\delta^{18}\text{O}$ of topsoil water decreased from -3 ‰ at the top of the 0–15 cm soil layer and then stabilized between -9 and -10 ‰ at the 15–30 cm soil layer; bedrock water was between -2 and -4 ‰ without significant differences between rock layers (Fig. 3a). In addition, soil pocket water had more negative $\delta^{18}\text{O}$ values than bedrock suggesting less evaporation and $\delta^{18}\text{O}$ of stem water was similar in both *G. floribundum* and *P. pispicula*

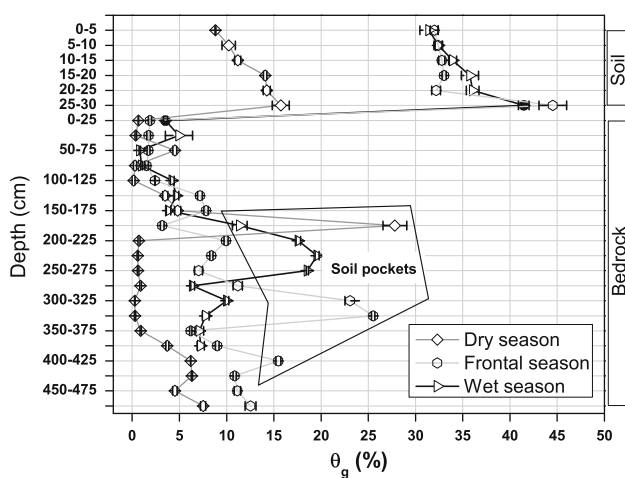


Fig. 2 Gravimetric water content (θ_g) of topsoil, bedrock and soil in pockets of the tree sampling campaigns at the quarry in northern Yucatan. Y axis shows different scales for topsoil (0–30 cm) and bedrock (0–500 cm)

(Fig. 3a). In the frontal season, $\delta^{18}\text{O}$ of topsoil water from 0 to 15 cm was -5 to -6 ‰ and then increased to -3 ‰ from 15 to 30 cm depth suggesting that a recent precipitation event affected mostly the top 15 cm of topsoil, and bedrock water $\delta^{18}\text{O}$ ranged from -1 to -3.5 ‰ at 0–225 cm depth and -3 to -5 ‰ deeper in the soil profile (Fig. 3b). Soil pockets were similar to bedrock and stem water $\delta^{18}\text{O}$ was higher in *G. floribundum* than *P. pispicula* (Fig. 3b). In the dry season, topsoil water between 0 and 15 cm was the source most affected by evaporation and showed enriched values above $+2$ ‰ (Fig. 3c). Bedrock water $\delta^{18}\text{O}$ ranged from -2 to -4 ‰ and stem water $\delta^{18}\text{O}$ was similar in *G. floribundum* and *P. pispicula* ranging from -1.5 to -2.5 (Fig. 3c). No soil pockets were found during the sampling of this wall.

In the frontal season, all water sources and stem water $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values kept near the meteoric water line, suggesting low evaporation rates; $\delta^{18}\text{O}$ values of *P. pispicula* and *G. floribundum* stem water were similar, with values corresponding to soil 0–15 cm (Fig. 3d). In the frontal season, topsoil 0–15 cm and stem water in *P. pispicula* showed more negative $\delta^{18}\text{O}$ and $\delta^2\text{H}$ than ground water, suggesting that unsampled precipitation from a cold front played an important role as a water source for these species (Fig. 3e). Stem water $\delta^{18}\text{O}$ was higher in *G. floribundum* than in *P. pispicula*, thus *P. pispicula* stem water was similar to a recent unmeasured precipitation event, whereas *G. floribundum* stem water was similar to 15–30 cm deep topsoil and deep bedrock water. In the dry season, $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values of trees and all water sources, except ground water, were to the right side of the Meteoric Water Line in the zone of strong evaporation effects (Fig. 3f).

Results of the Iso-source model indicate that soil water between 15 and 30 cm depth was the most important source for *P. pispicula*, whereas soil 0–15 cm, soil 15–30 cm, and especially rock 200–500 cm were the most important sources for *G. floribundum* (Table 2).

Growth, phenology and leaf measurements

Piscidia pispicula had twice the crown area and height, fewer trunks and approximately three times the DBH of *G. floribundum*; *P. pispicula* also showed greater RGR_{Height} ($p = 0.01$) and RGR_{DBH} ($p = 0.08$) than *G. floribundum* (Table 3). Phenology varied between the two species, with *G. floribundum* shedding leaves in December, the driest month of the year, and new leaves generated in February, after several precipitation events associated with cold fronts (Fig. 4). Total flush of leaves occurred in 3 months with a period where shedding and regrowth occurred at the same time. *P. pispicula* leaf fall started in April, 1 month before the end of the dry season, and produced new leaves

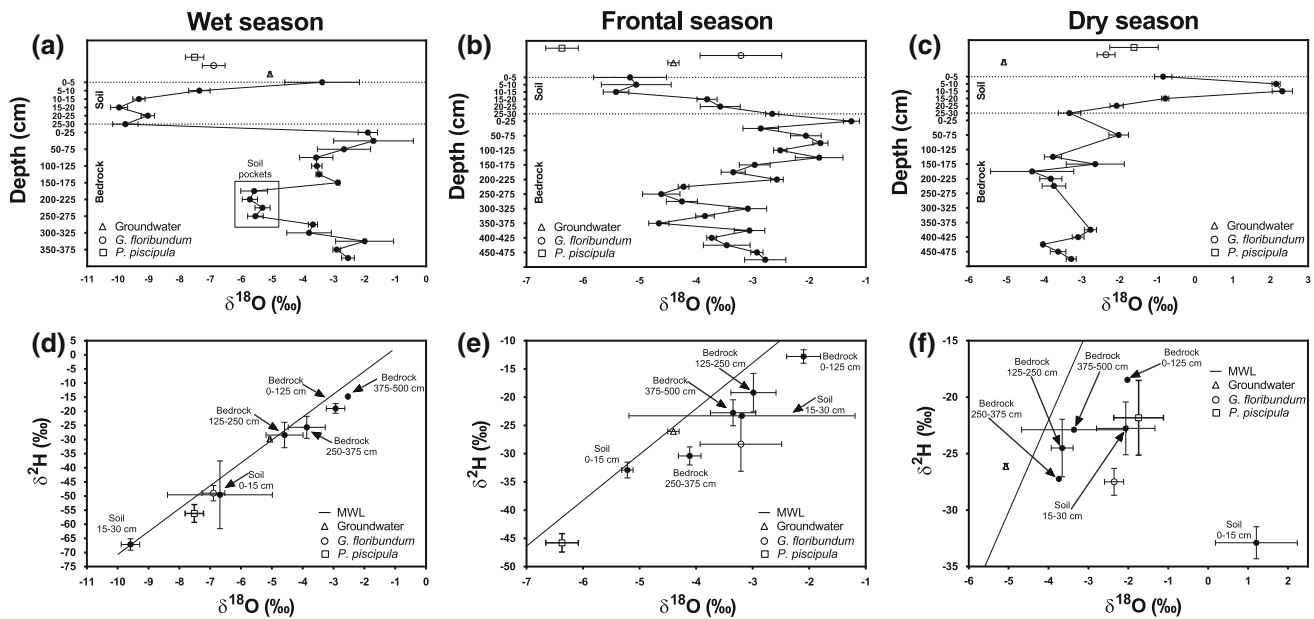


Fig. 3 $\delta^{18}\text{O}$ isotopic values of soil/rock profile, groundwater and stem water of *P. piscipula* and *G. floribundum* in wet season 2007 (a), frontal season 2008 (b) and dry season 2008 (c). Y axis shows different scales for topsoil (0–30 cm) and bedrock (0–500 cm). Mean values \pm SE (b). $\delta^2\text{H}$ vs $\delta^{18}\text{O}$ values from *P. piscipula* and *G.*

floribundum trees, topsoil water, bedrock water and groundwater in wet season 2007 (d), frontal season 2008 (e) and dry season 2008 (f). Fitted line is the meteoric water line (MWL) by Socki et al. (2002) ($\delta^2\text{H} = 8.11\text{X } \delta^{18}\text{O} + 10.4$)

Table 2 Water percentage contributions to *P. piscipula* and *G. floribundum* of the different water sources calculated with the Iso-source software

Sources	<i>P. piscipula</i>		<i>G. floribundum</i>	
	Wet season 2007	Dry season 2008	Wet season 2007	Dry season 2008
Soil 0–15 cm	9–65	0	0–74	1–22
Soil 15–30 cm	35–67	96–100	14–54	0–26
Rock 200–500 cm	0–24	0–4	12–46	59–90

Table 3 Phenological characterization, morphology and relative growth rate of height (RGR_{Height}) and diameter at breast height (RGR_{DBH}) of *Gymnopodium floribundum* and *Piscidia piscipula* trees growing on karst substrate in Northern Yucatan, Mexico. Mean \pm SE, $n = 5$

	<i>G. floribundum</i>	<i>P. piscipula</i>
Leaf phenology	Early deciduous	Late deciduous
Crown area (m ²)	10.1 \pm 3.2	23.4 \pm 4.2
Number of trunks (range)	4–7	2–3
Initial height (m)	462 \pm 13	794 \pm 56
RGR _{Height} (cm cm ⁻¹ day ⁻¹)	1.6 \pm 0.4	2.09 \pm 0.07
Initial DBH* (cm)	5.6 \pm 1.6	15.9 \pm 3.5
RGR _{DBH} (cm cm ⁻¹ day ⁻¹)	1.73 \pm 0.2	2.76 \pm 0.2

with the beginning of the wet season. Total flush of leaves occurred in 4 months (Fig. 4).

Leaf fall showed three main peaks for both species (Fig. 5). The first two peaks occurred at the same time for both species (September and December) while the third one occurred earlier in *G. floribundum* (March) and one month later in *P. piscipula*. The maximum leaf fall value observed was in December for *P. piscipula* and in March for *G. floribundum*. The effects of species ($p = 0.03$) and month ($p < 0.0001$) were both highly significant for litterfall and showed a significant interaction ($p = 0.001$).

Except for the dry season, leaf size was greater in *P. piscipula* than in *G. floribundum* ($p = 0.01$; Fig. 6). For most of the year, leaves of *P. piscipula* were twice as large as those of *G. floribundum*. The minimum leaf size value for *P. piscipula* was 9 cm² and for *G. floribundum* was 5 cm², both occurring at the beginning of the wet season. Then, *P. piscipula* leaf size progressively increased to a maximum of 20 cm² in February to decrease again during the last part of the dry season, when leaf shedding occurred. On the other hand, *G. floribundum* experienced a leaf growth increment of 3 cm² in July and then remained relatively constant with values ranging between 8 and 10 cm².

Water potential varied between species on the three sampling campaigns. *G. floribundum* always had more positive values than *P. piscipula* ($p < 0.001$; Fig. 7). The most positive Ψ_{PD} values for both species were recorded in

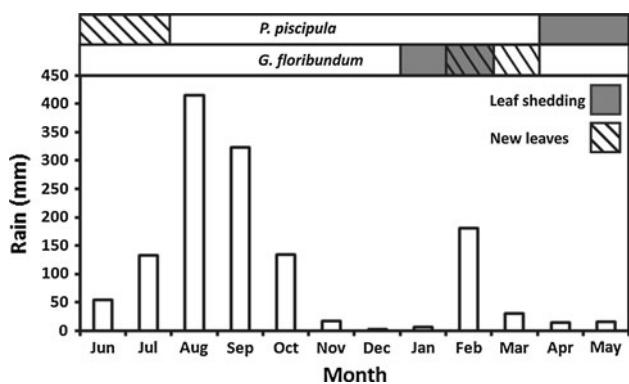


Fig. 4 Phenology of *P. piscipula* and *G. floribundum* species and precipitation at the quarry in northern Yucatan

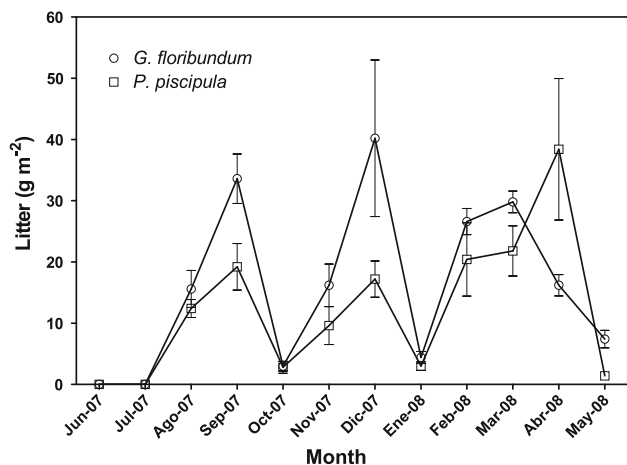


Fig. 5 Total leaf fall of *G. floribundum* and *P. piscipula* at the quarry in northern Yucatan. Mean ± SE

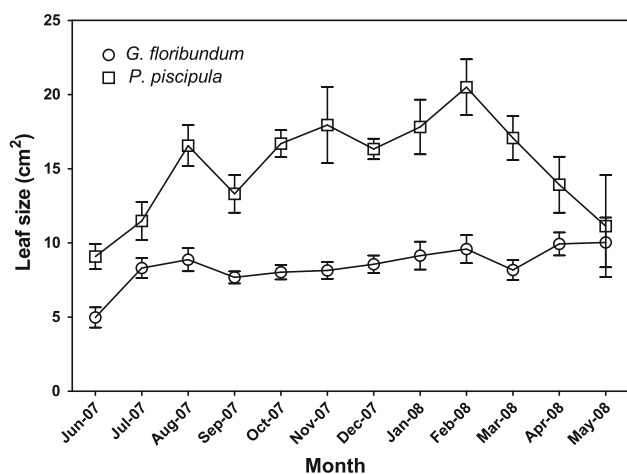


Fig. 6 Leaf size of *G. floribundum* and *P. piscipula* growing at the quarry in northern Yucatan. Mean ± SE

the wet season and the most negative in the frontal season. The most pronounced difference between Ψ_{PD} and Ψ_{MD} for both species was in the frontal season, while similar

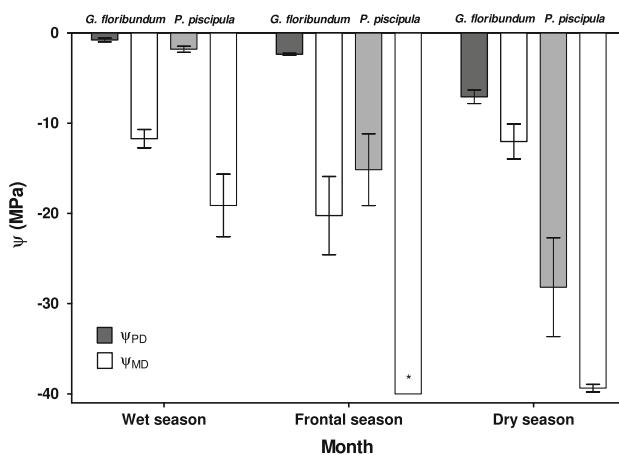


Fig. 7 Predawn (Ψ_{PD}) and Midday (Ψ_{MD}) water potentials of *G. floribundum* and *P. piscipula* trees at the quarry in northern Yucatan. Mean ± SE. Asterisk error bar not provided because most of the samples were out of the measurement range of the Scholander pressure chamber used (4 MPa)

Ψ_{PD} and Ψ_{MD} values were recorded, for both species, during the dry season. Some *G. floribundum* trees had values off the scale of the pressure chamber used (4 MPa). These results agreed with precipitation values that show January as the second driest month of the year. In the dry season, *G. floribundum* had lower values for both Ψ_{PD} and Ψ_{MD} compared with the previous sampling campaign whereas *P. piscipula* had roughly similar values.

Bulk leaf organic $\delta^{13}C$ of *G. floribundum* and *P. piscipula* had similar patterns through the year (Fig. 8a). However, *G. floribundum* presented three peaks occurring in September, March and June, all related to wet periods. *P. piscipula* only seemed to respond to the beginning of the wet season. In both species $\delta^{13}C$ reached minimum values during December, the driest month of the year.

Leaf $\delta^{18}O$ showed a similar trend in both species with *G. floribundum* having higher values than *P. piscipula* (Fig. 8b). *G. floribundum* showed a small decrease of the foliar $\delta^{18}O$ composition in February which is probably related to its leaf shedding occurring that month. There were also low values ($\approx 28\text{‰}$) in April which represents the dry season. Overall, leaf organic $\delta^{18}O$ and $\delta^{13}C$ increased during the dry season in both species compared to the wet season (Fig. 8c). There was a significant correlation between leaf organic $\delta^{18}O$ and $\delta^{13}C$ within each species with a more pronounced slope in *P. piscipula* (Fig. 8d).

Discussion

Our results show that the greatest variation in stem water $\delta^{18}O$ and plant water sources occurred during the frontal season and initiation of the dry season in February, when

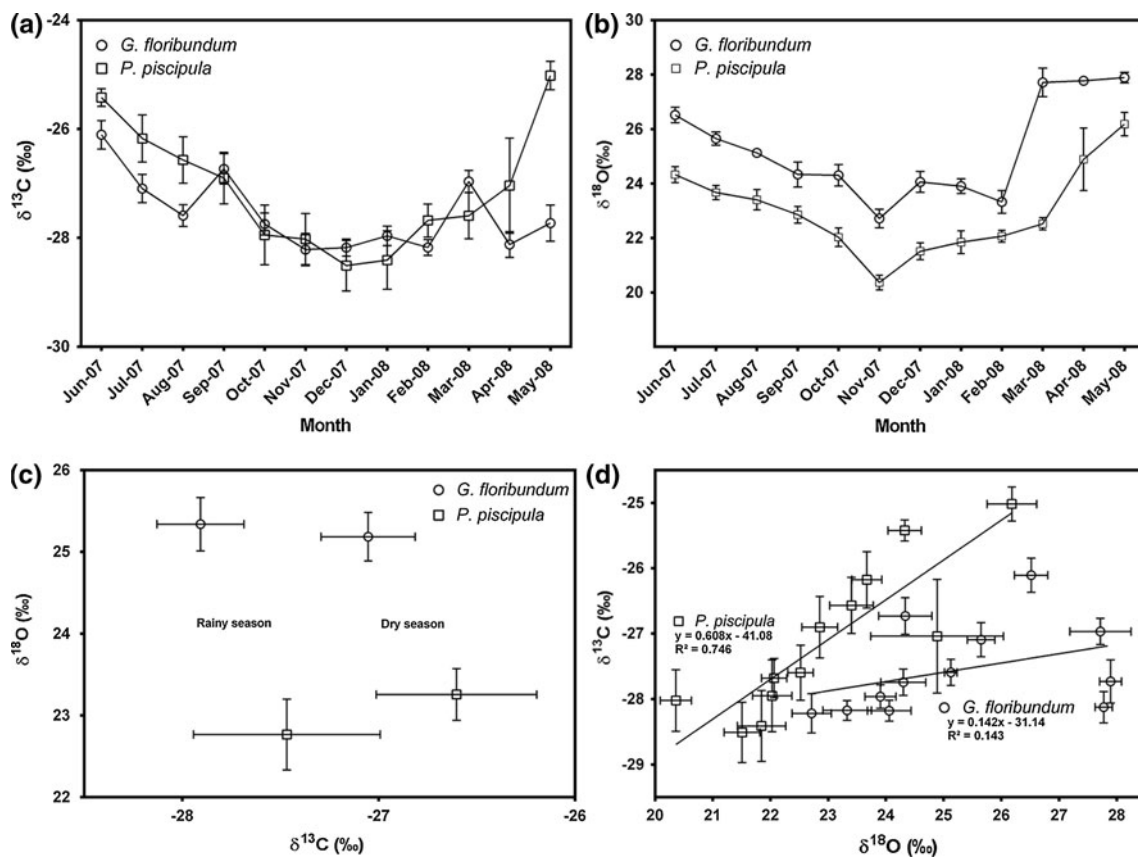


Fig. 8 Leaf $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ compositions of *G. floribundum* and *P. piscipula* trees. **a** $\delta^{13}\text{C}$; **b** $\delta^{18}\text{O}$; **c** $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ during the wet and dry seasons; **d** Monthly $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ regressions. Mean \pm SE

G. floribundum was shedding old leaves and growing new leaves, but *P. piscipula* maintained its leaves from the previous wet season (Figs. 3b, e, 4). Contrary to what was expected, *P. piscipula* took water primarily from shallow sources regardless of the month, although some contribution from deeper sources has the potential to occur. Rain also appeared to be an important source for this species. This implies that *P. piscipula* could have a very well-developed shallow root system that allows rapid water uptake after a precipitation event. On the other hand, *G. floribundum* took water from topsoil and bedrock, the latter being a more important source in the dry season. This suggests a deeper root system than *G. floribundum*. Overall, our results indicate that the contrasting early and late dry season leaf loss phenology of these two species is not simply determined by rooting depth, but rather a more complicated suite of species-based characteristics based on opportunistic use of dynamic water sources, the balance between carbon gain and water loss, and maintenance of water potential at the end of the dry season. These results are consistent with other studies demonstrating a broad array of coordinated strategies for dealing with seasonal drought in tropical forests (Santiago et al. 2004; Pineda-García et al. 2012).

A primary factor determining differences in leaf loss phenology between the two studied species appears to be the maintenance of water potential. *G. floribundum* consistently exhibited more positive water potential values than *P. piscipula*, suggesting that *G. floribundum* has a limited capacity to tolerate negative water potential and moderates water use in a manner that maintains bulk leaf water potential at relatively more positive values compared to *P. piscipula* (Fig. 7). This could provide an advantage of maximizing carbon gain during the dry season when light availability is high (Wright and van Schaik 1994). Leaf organic $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values support this observation, because *P. piscipula* showed consistently higher $\delta^{13}\text{C}$ values than *G. floribundum* (Fig. 8b), coupled with lower $\delta^{18}\text{O}$ indicating that the decrease in photosynthetic carbon isotope discrimination was associated with greater stomatal conductance and greater photosynthesis (Scheidegger et al. 2000). Greater photosynthesis in *P. piscipula* is consistent with maintaining a canopy of leaves later into the dry season. Thus, our results are most consistent with maintenance plant water potential to maximize carbon gain during the onset of the dry season.

The observation that *P. piscipula* appeared to use shallower water sources and maintained its canopy of leaves

later into the dry season was not expected. Part of this pattern is driven by the capability of *P. piscipula* to utilize dynamic sources of water, such as the cold front precipitation during the frontal season (Fig. 3b). This makes sense, because the *Laja* bedrock layer was a poor source of water at all times, and soil pockets, which are available, but heterogeneous in distribution, were always better sources of water than rock layers (Fig. 2). Water content of soil/bedrock sources changed along the year suggesting a different seasonal contribution to plant water uptake. The θ_g of topsoil in the wet and frontal seasons were very similar and three times greater than values measured in the dry season. The *Sascab* bedrock layer could be a significant source of water in the wet and frontal seasons, but not in the dry season. Soil pockets had two times more water than topsoil in the dry season suggesting that they could be an important source of water for trees during the dry season. In the dry season, the rock profile had θ_g between 1 and 5 % but nearly all were less than 1 %. These values were slightly lower than those reported by Querejeta et al. (2006, 2007) and Hasselquist et al. (2010) in nearby areas, which suggest that the bedrock was subjected to a greater evaporation during this study.

The $\delta^{18}\text{O}$ values of water in this study integrated processes ranging from evaporation of soil and bedrock water sources, transpiration of tree species, and precipitation events. In the wet season, enriched values of $\delta^{18}\text{O}$ of water in topsoil 10–15 cm and trees revealed the occurrence of a depleted precipitation event that occurred on October 21, 1 day before sampling, bringing 19.7 mm of water (Servicio Meteorológico Nacional 2007). Furthermore, a frontal system including cold front #3, the tropical wave #37, as well as the remnants of tropical storm *Kiko* that formed in the Pacific, converged on the study area days before the wet season sampling in October 2007 (CONAGUA 2007). Hurricanes, tropical storms and cold fronts generally have lower stable isotope ratios than convective precipitation events (Lawrence and Gedzelman 1996; Price et al. 2008). For example, Perry et al. (2003) recorded $\delta^{18}\text{O}$ values of -9.91 ‰ for precipitation during tropical storm *Mitch* in 1998, and precipitation events ranging from -6 to -10 ‰ for $\delta^{18}\text{O}$ have been recorded in the vicinities of the study area (IAEA 2001). Consequently, depleted oxygen values in soil 15–30 cm and *P. piscipula* and *G. floribundum* trees could be accredited to precipitation originated from these events. Soil pockets also showed more negative values than rock, suggesting that depleted rain water reached this layer.

During dry season measurements in February 2008, the $\delta^{18}\text{O}$ of topsoil 0–15 cm was more positive than ground-water suggesting another depleted source of water. Cold front #29, which occurred 4 days before sampling and brought 33.9 mm (CONAGUA 2008; Servicio Meteorológico Nacional 2008), could be the main source of water.

The strength of the dry season promoted the enrichment of all water sources respect to earlier samplings. However, the more negative value of topsoil from 0 to 5 cm could be affected by dew water since this soil sampling was done early in the morning. More negative $\delta^{18}\text{O}$ values in topsoil than ground water have also been observed by Saha et al. (2009) in similar environmental conditions in Miami, associated with water condensation occurring at night in the upper soil layers. Condensation has been shown to deplete $\delta^{18}\text{O}$ soil water 10–15 cm depth by 5 ‰ (Takahashi 1998). Condensation can also account for up to 47 % of total transpiration (de Jong 2005). Surface dew is easily generated when temperatures go below the dew point at night or in early morning (Andrade 2003; Zhang et al. 2009). Under tropical conditions in Tahiti, Clus et al. (2008) reported average dew yields of 0.102 mm of dew during the dry season. Therefore, condensed water could be an important source for *P. piscipula*. Overall, our results indicate that variation in phenology between these two deciduous tropical dry-forest tree species, which vary in the timing of their deciduousness, is not akin to the relatively large variation in rooting depth that can occur between tropical evergreen and deciduous species (Jackson et al. 1995), but rather reflects the diversity of plant physiological strategies that occur in tropical forest (Meinzer et al. 2008).

Conclusions

Soil pockets can hold a similar amount of water as topsoil, except during the dry season when topsoil gets dry. Rocks hold lower amounts of water than topsoil at all times; however, *sascab* rock, along with soil pockets, is an important source of water for *G. floribundum*.

P. piscipula showed greater $\text{RGR}_{\text{Height}}$ and RGR_{DBH} , lower litter fall, larger leaf size, lower $\delta^{18}\text{O}$ and higher isotopic WUE. These differences in phenology, growth and WUE seem to be related to their strategy to control water potential. *P. piscipula* trees maintain greater water content at all times and tolerate more negative water potentials compared to *G. floribundum*.

The contrasting early and late dry season leaf loss phenology of these two species is not simply determined by rooting depth, but rather a more complicated suite of characteristics based on opportunistic use of dynamic water sources, maximizing carbon gain, and maintenance of water potential during the dry season.

Acknowledgments We thank to CONACyT-UCMEXUS for the scholarship granted to the first author for doctoral studies at the University of California Riverside. This work was supported by UCMEXUS through the projects: “Importance of limestone bedrock and subsurface pockets of soil as potential sources of water for dry

deciduous tree species in northern Yucatán” and “Water contribution by limestone bedrock and subsurface SP and its effect on the water use efficiency of two tree species in Yucatan, Mexico”; grants from the National Science Foundation (DEB 0615427, DEB 0770 6813, EF 0410408, and CRR 0120778), and the UCR Center for Conservation Biology. We would like to thank the owners of the quarry, especially Héctor Buenfil Cervera; the workers of the quarry, especially Roger Armando Fernández Paredes, and Augusto Cervera Buenfil for helping with the work logistics; Alfonso Castillo, María José Romero, Raúl Hernandez and Ariel Esparza for helping with the field and laboratory work.

References

- Allison GB, Barnes CJ, Hughes MW (1983) The distribution of Deuterium and O-18 in dry soils. 2. Experimental. *J Hydrol* 64:377–397
- Andrade JL (2003) Dew deposition on epiphytic Bromeliad leaves: an important event in a Mexican tropical dry deciduous forest. *J Trop Ecol* 19:479–488
- Barbour MM (2007) Stable oxygen isotope composition of plant tissue: a review. *Funct Plant Biol* 34:83–94
- Barbour MM, Fischer RA, Sayre KD, Farquhar GD (2000) Oxygen isotope ratio of leaf and grain material correlates with stomatal conductance and grain yield in irrigated wheat. *Aust J Plant Physiol* 27:625–637
- Chemás A, Rico-Gray V (1991) Apiculture and management of associated vegetation by the maya of Tixcaltuyub, Yucatán, México. *Agrofor Syst* 13:13–25
- Clus O, Ortega P, Muselli M, Milimouk I, Beysens D (2008) Study of dew water collection in humid tropical islands. *J Hydrol* 361:159–171
- CONAGUA (2000) Normales climatológicas del municipio de Mérida, Yucatán en el periodo 1981–2000 http://smn.cna.gob.mx/index.php?option=com_content&view=article&id=29:resumen-historico&catid=1:general&Itemid=93
- CONAGUA (2007) Bitácora Meteorológica No. 010. Octubre 2007. Servicio Meteorológico Nacional, México. <http://smn.cna.gob.mx/boletin/bitacora/bitacora-feb08.html>
- CONAGUA (2008) Bitácora Meteorológica No. 02. Febrero 2008. Servicio Meteorológico Nacional, México. <http://smn.cna.gob.mx/boletin/bitacora/bitacora-feb08.html>
- de Jong C (2005) The contribution of condensation to the water cycle under high-mountain conditions. *Hydrol Process* 19:2419–2435
- Do FC, Goudiaby VA, Gimenez O, Diagne AL, Diouf M, Rocheteau A, Akpo LE (2005) Environmental influence on canopy phenology in the dry tropics. *Forest Ecol Manage* 215:319–328
- Eamus D (1999) Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends Ecol Evol* 14:11–16
- 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 ecosystemlevel water relation through stable isotope analyses. In: Sala OE, Jackson RB, Mooney HA, Howarth RW (eds) *Methods in ecosystem science*. Springer, New York, pp 181–198
- Estrada-Medina H, Graham RC, Allen MF, Jiménez-Osornio JJ (2010) The importance of limestone bedrock and dissolution karst features on tree root distribution in northern Yucatán, México. *Vadose Zone* 9:653–661
- Estrada-Medina H, Graham RC, Allen MF, Jiménez-Osornio JJ, Robles-Casolco S (2013) The role of limestone bedrock and dissolution karst features on tree root distribution in northern Yucatán, México. *Plant Soil* 362:37–50
- Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. *Annu Rev Plant Physiol Plant Mol Biol* 40:503–537
- González-Iturbe JA, Olmsted I, Tun-Dzul F (2002) Tropical dry forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan, Mexico. *Forest Ecol Manag* 167:67–82
- Hasselquist N, Allen M, Santiago L (2010) Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence. *Oecologia* 164:881–890
- Hoffmann WA, Poorter H (2002) Avoiding bias in calculations of relative growth rate. *Ann Bot* 90(1):37–42
- Holbrook M, Whitbeck J, Mooney H (1995) Drought responses of neotropical dry forest trees. In: Bullock SH, Mooney HA, Medina E (eds) *Seasonally dry tropical forests*. Cambridge University Press, Cambridge
- IAEA (2001). GNIP Maps and Animations, International Atomic Energy Agency, Vienna. Accessible at <http://isohis.iaea.org>
- Jackson PC, Cavelier J, Goldstein G, Meinzer FC, Holbrook NM (1995) Partitioning of water resources among plants of a lowland tropical forest. *Oecologia* 101:197–203
- Lambers H, Chapin FS, Pons TL (1998) *Plant physiological ecology*. Springer, New York
- Lawrence RJ, Gedzelman DS (1996) Low stable isotope ratios of tropical cyclone rains. *Geophys Res Lett* 23:527–530
- Lobo JA, Quesada M, Stoner KE, Fuchs EJ, Herreri-as-Diego Y, Rojas J, Sabori-o G (2003) Factors affecting phenological patterns of bombacaceous trees in seasonal forests in Costa Rica and Mexico. *Am J Bot* 90:1054–1106
- McCulley RL, Jobbágy EG, Pockman WT, Jackson RB (2004) Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems. *Oecologia* 141:620–628
- McMahon MJ, Christy AD (2000) Root growth, calcite precipitation, and gas and water movement in fractures and macropores: a review with field observations. *Ohio J Sci* 100:88–93
- Meinzer FC, Andrade JL, Goldstein G, Holbrook M, Cavelier J, Wright J (1999) Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* 121:293–301
- Meinzer FC, Woodruff DR, Domec JC, Goldstein G, Campanello PI, Gatti MG, Villalobos-Vega R (2008) Coordination of leaf and stem water transport properties in tropical forest trees. *Oecologia* 156:31–41
- 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
- Nelson G (1994) *The trees of Florida: a reference and field guide*. Pineapple Press, Sarasota
- 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 Ordoñez J, Chico Ponce de León P (eds) *Atlas de Procesos Territoriales de Yucatán*. Universidad Autónoma de Yucatán, Mérida, pp 163–182
- Ortiz, JJ (1994) *Etnoflora Yucatanense*. Polygonaceae. Universidad Autónoma de Yucatán. Fascículo 10
- Perry E, Velazquez-Oliman G, Socki RA (2003) Hidrogeology of the Yucatan Peninsula. In: Gomez-Pompa A, Allen MF, Fedick SL, Osornio JJ (eds) *The Lowland Maya area: three millennia at the human-wildland interface*. Food Products Press, Binghamton
- Phillips DL, Gregg JW (2003) Source partitioning using stable isotopes: coping with too many sources. *Oecologia* 136:261–269
- Phillips D, Newsome S, Gregg J (2005) Combining sources in stable isotope mixing models: alternative methods. *Oecologia* 144:520–527

- Pineda-García F, Paz H, Meinzer FC (2012) Drought resistance in early and late secondary successional species from a tropical dry forest: the interplay between xylem resistance to embolism, sapwood water storage and leaf shedding. *Plant Cell Environ*. doi:10.1111/j.1365-3040.2012.02582
- Price RM, Swart PK, Willoughby HE (2008) Seasonal and spatial variation in the stable isotopic composition ($\delta^{18}\text{O}$ and $\delta^2\text{H}$) of precipitation in South Florida. *J Hydrol* 358:193–205
- Querejeta J, Estrada-Medina H, Allen M, Jiménez-Osornio JJ, Ruess R (2006) Utilization of bedrock water by *Brosimum alicastrum* trees growing on shallow soil atop limestone in a dry tropical climate. *Plant Soil* 287:187–197
- Querejeta J, Estrada-Medina H, Allen M, Jiménez-Osornio JJ (2007) Water source partitioning among trees growing on shallow karst soils in a seasonally dry tropical climate. *Oecologia* 152:26–36
- Rico-Gray V, Chemás A, Mandujano S (1991) Uses of tropical deciduous forest species by the Yucatecan Maya. *Agrofor Syst* 14:149–161
- Roden JS, Ehleringer JR (1999) Hydrogen and oxygen isotope ratios of tree-ring cellulose for riparian trees grown long-term under hydroponically controlled environments. *Oecologia* 121:467–477
- Saha AK, da Stenberg LSL, Miralles-Wilhelm F (2009) Linking water sources with foliar nutrient status in upland plant communities in the Everglades National Park, USA. *Ecohydrology* 2:42–54
- Santiago LS, Kitajima K, Wright SJ, Mulkey SS (2004) Coordinated changes in photosynthesis, water relations and leaf nutritional traits of canopy trees along a precipitation gradient in lowland tropical forest. *Oecologia* 139:495–502
- Scheidegger Y, Saurer M, Bahn M, Siegwolf R (2000) Linking stable oxygen and carbon isotopes with stomatal conductance and photosynthetic capacity: a conceptual model. *Oecologia* 125:350–357
- Servicio Meteorológico Nacional (2007) Resumen mensual meteorológico. Octubre 2007. Estación Mérida-Aeropuerto, Yucatán
- Servicio Meteorológico Nacional (2008) Resumen mensual meteorológico. Febrero, 2008. Estación Mérida-Aeropuerto, Yucatán
- Socki RA, Perry EC Jr, Romanek CS (2002) Stable isotope systematics of two cenotes from the northern Yucatan Peninsula, Mexico. *Limnol Oceanogr* 47:1808–1818
- Standley PC (1930) Flora of the Yucatán. Publication 279. Botanical Series, Vol III, No. 3. Field Museum of Natural History Chicago
- Standley PC, Steyermark JA (1946). Polygonaceae. In: Standley PC, Steyermark JA (Eds) Flora of Guatemala-Part IV. Fieldiana Botany, vol 24, issue no. 4, pp 104–137
- Takahashi K (1998) Oxygen isotope ratios between soil water and stem water of trees in pot experiments. *Ecol Res* 13:1–5
- Tyree MT, Vargas G, Engelbrecht BMJ, Kursar TA (2002) Drought until death do us part: a case study of the desiccation-tolerance of a tropical moist forest seedling-tree, *Licania platypus* (Hemsl.) Fritsch. *J Exp Bot* 53:2239–2247
- Tyree MT, Engelbrecht BMJ, Vargas G, Kursar TA (2003) Desiccation tolerance of five tropical seedlings in Panama. Relationship to a field assessment of drought performance. *Plant Physiol* 132:1439–1447
- West AG, Patrickson SJ, Ehleringer JR (2006) Water extraction times for plant and soil materials used in stable isotope analysis. *Rapid Commun Mass Spectrom* 20:1317–1321
- Williams RJ, Myers BA, Muller WJ, Duff GA, Eamus D (1997) Leaf phenology of woody species in a North Australian Tropical Savanna. *Ecology* 78:2542–2558
- Wright SJ, van Schaik CP (1994) Light and the phenology of tropical trees. *Am Nat* 143:192–199
- Zalamea M (2008) Leaf fall phenology in a subtropical wet forest in Puerto Rico: from species to community patterns. *Biotropica* 40(3):295–304
- Zhang XP, Yang ZL, Niu GY, Wang XY (2009) Stable water isotope simulation in different reservoirs of Manaus, Brazil, by community land model incorporating stable isotopic effect. *Int J Climatol* 29:619–628