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Functional strategies of tropical dry forest plants in relation to growth form and isotopic composition

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Abstract

Tropical dry forests (TDFs) undergo a substantial dry season in which plant species must endure several months of drought. Although TDFs support a diverse array of plant growth forms, it is not clear how they vary in mechanisms for coping with seasonal drought. We measured organic tissue stable isotopic composition of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) across six plant growth forms including epiphytes, terrestrial succulents, trees, shrubs, herbs, and vines, and oxygen ($\delta^{18}\text{O}$) of four growth forms, to distinguish among patterns of resource acquisition and evaluate mechanisms for surviving annual drought in a lowland tropical dry forest in Yucatan, Mexico. Terrestrial succulent and epiphyte $\delta^{13}\text{C}$ was around -14‰ , indicating photosynthesis through the Crassulacean acid metabolism pathway, and along with one C_4 herb were distinct from mean values of all other growth forms, which were between -26 and -29‰ indicating C_3 photosynthesis. Mean tissue $\delta^{15}\text{N}$ across epiphytes was -4.95‰ and was significantly lower than all other growth forms, which had values around $+3\text{‰}$. Tissue N concentration varied significantly among growth forms with epiphytes and terrestrial succulents having significantly lower values of about 1% compared to trees, shrubs, herbs and vines, which were around 3%. Tissue C concentration was highest in trees, shrubs and vines, intermediate in herbs and epiphytes and lowest in terrestrial succulents. $\delta^{18}\text{O}$ did not vary among growth forms. Overall, our results suggest several water-saving aspects of resource acquisition, including the absolute occurrence of CAM photosynthesis in terrestrial succulents and epiphytes, high concentrations of leaf N in some species, which may facilitate CO_2 drawdown by photosynthetic enzymes for a given stomatal conductance, and potentially diverse N sources ranging from atmospheric N in epiphytes with extremely depleted $\delta^{15}\text{N}$ values, and a large range of $\delta^{15}\text{N}$ values among trees, many of which are legumes and dry season deciduous.

1. Introduction

Tropical dry forests (TDF) occur on the driest edges of the lowland tropics. These forests often respond to an extended seasonal drought with much of the canopy tree species losing their leaves (Chabot and Hicks 1982, Santiago *et al* 2004). However, these forests also support evergreen trees that maintain physiological activity during the dry season, as well as other growth forms such as succulent plants and a burst of herbaceous

vegetation during the short wet season, indicating a diversity of mechanisms for coping with seasonal drought (Pivovarov *et al* 2016, Santiago *et al* 2016). For canopy trees, drought survival mechanisms may include deep rooting, careful gas exchange, or the ability to shed leaves during the dry season (Hasselquist *et al* 2010), whereas for other growth forms, drought survival may involve water-saving modes of photosynthesis such as crassulacean acid metabolism (CAM) or C_4 photosynthesis (Ehleringer and Monson 1993,

Benzing 2008, Valdez-Hernández *et al* 2015). We measured stable isotopes on organic tissue of six growth forms of TDF plants to distinguish among patterns of resource acquisition and evaluate mechanisms for surviving the annual dry season.

One of the primary ways in which stable isotopes can provide information is through the use of carbon isotopic composition ($\delta^{13}\text{C}$) to identify photosynthetic pathways (Bender 1971). Whereas most plant species exhibit C_3 photosynthesis, CAM and C_4 photosynthesis are thought to have evolved as water saving modes of photosynthesis, with C_4 plants exhibiting a spatial separation of carboxylation and CAM exhibiting a temporal separation of carboxylation, both of which increase carbon gain per water lost (Ehleringer and Monson 1993). There is no overlap in $\delta^{13}\text{C}$ between plants with C_3 and C_4 photosynthetic pathways, with C_3 plants having values in the -20 to -35‰ range and C_4 plants having values in the -7 to -15‰ range (Ehleringer and Osmond 1989, Dawson *et al* 2002). In contrast, $\delta^{13}\text{C}$ in CAM plants can vary from about -10 to -22‰ (Ehleringer and Monson 1993, Santiago *et al* 2005, Silvera *et al* 2005), depending on the contribution of C_3 photosynthesis during the light phase of the CAM cycle (Winter and Holtum 2002), yet many CAM plants are easily recognizable by their succulent tissue (Andrade *et al* 2007). Within C_3 plant species, $\delta^{13}\text{C}$ also provides information on carbon acquisition because the supply of CO_2 at the site of carboxylation determines discrimination against $^{13}\text{CO}_2$ relative to $^{12}\text{CO}_2$ during photosynthesis (Farquhar and Richards 1984), and when stomatal conductance is low, CO_2 is generally more scarce, so assimilation of $^{13}\text{CO}_2$ increases, resulting in tissue with greater $\delta^{13}\text{C}$ values (Cernusak *et al* 2013).

Analysis of tissue N concentration and N stable isotopic composition can also provide information on resource acquisition. A high tissue N concentration could benefit TDF plants by enabling high rates of photosynthesis and maximizing carbon gain opportunities during the short wet season (Givnish 2002). Additionally, a high tissue N concentration has the potential to maximize carbon gain for a given stomatal conductance (Wright *et al* 2003), during water deficit. N isotopic composition ($\delta^{15}\text{N}$) of plant tissue reflects N sources, and alternative N sources such as biological N_2 -fixation or atmospheric deposition of N might allow contrasting growth forms unique mechanisms for supporting carbon gain (Boddey *et al* 2000, Craine *et al* 2015).

We also explored the use of tissue oxygen stable isotopic composition ($\delta^{18}\text{O}$). Values for $\delta^{18}\text{O}$ are able to provide information on water loss through stomata and can aid in distinguishing among patterns of gas exchange because higher values indicate greater evaporative enrichment, which is normally caused by lower vapor pressure deficit or tighter stomatal control (Scheidegger *et al* 2000, Cernusak *et al* 2008). Our main questions were: (1) What is the range of

stable isotopic composition and concentration of C, N and O among a broad array of TDF plant species? (2) Is there correspondence between stable isotope values and the major growth forms of TDFs? (3) Do stable isotope patterns reveal physiological mechanisms for coping with seasonal and long-term drought? We hypothesized large ranges in isotopic composition and concentration of C, N and O in this forest, given the diversity of growth forms, phenology and the strong seasonality of the site. We also expected significant differences in isotopic composition of all elements among growth forms, based on their apparent contrasting patterns of carbon, water and mineral nutrient acquisition. Finally, we anticipated that isotope analysis would reveal possible physiological mechanisms for coping with drought, including alternative photosynthetic pathways in epiphytes and succulents, and alternative N sources such as atmospheric deposition in epiphytes and biological N_2 -fixation in leguminous trees.

2. Methods

2.1. Study site

The study was conducted in the northwest Yucatan Peninsula in Dzibilchaltún National Park (21.0910°N , 89.5903°W). The site receives approximately 760 mm of precipitation annually with a long 8 month dry season in October–May in which there is < 100 mm per month, and a short a 4 month wet season in June–September. The average temperature is 26°C . The vegetation is classified as low deciduous forest 4–6 m in height with columnar cacti in the understory (Miranda and Hernández-X 1963). Mean range in soil depth is 5–50 cm (Ceccon *et al* 2002) on highly organic soil above the porous, calcareous parent material (Duch 1988). The site was a Mayan city dating back approximately 2500 years, but had more recently been used for industrial cultivation of *Agave fourcroydes* for fiber. The site is currently a mosaic of forest ages ranging from 10 to 50 years after agricultural abandonment and fire (González-Iturbe *et al* 2002).

2.2. Study species

Sixty-eight plant species from six growth forms including: (1) epiphytes (species growing on other plants with no roots reaching the soil), (2) terrestrial succulents (cacti and agaves), (3) trees (monopodial woody species), (4) shrubs (polypodial woody species), (5) herbs (herbaceous species of forest understory and clearings), and (6) vines (soil rooted species using other plants for support), were selected for study (table S1 available at stacks.iop.org/ERL/12/115006/mmedia). Nomenclature for this group of species is based on the Floristic List of the Yucatan Peninsula (Durán *et al* 2000), local expert knowledge on orchids (Germán Carnevali, personal communication), and the Missouri Botanical Garden Website (www.mobot.org).

2.3. Sample collection

Leaf tissue from epiphytes, trees, shrubs, herbs and vines, and aboveground green tissue from terrestrial succulents were collected throughout the wet season of 2004 (June–September), when all species had leaves and were physiologically active. Between three and nine individuals of each species were sampled and leaves were collected in the highest light availability in which a species usually occurs, including sunlit canopy leaves for canopy trees and terminal mature leaves for understory species. Samples were dried for 48 h at 65 °C or until constant mass and ground to a fine powder. All tissue samples from the same individual were pooled for chemical analysis. For all tissue samples, C and N concentrations and isotopic composition of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) were determined with an elemental analyzer (Model ANCA-SL, Europa Scientific, Ltd, Crewe, UK) connected to a continuous flow isotope ratio mass spectrometer (Model 20/20 Mass Spectrometer; PDZ Europa Scientific, Ltd.). We also measured oxygen isotopic composition ($\delta^{18}\text{O}$) on a subset of samples from three individuals of 20 species using a Finnigan MAT Delta PlusXL (Finnigan MAT, Bremen, Germany). All $\delta^{13}\text{C}$ values are expressed in delta notation (‰) relative to the internationally accepted standards for C (PeeDee Belemnite, PDB), N (Atmosphere, Atm), and O (Vienna Standard Mean Ocean Water, V-SMOW). All samples were measured at the University of California Center for Stable Isotope Biogeochemistry, Berkeley, California, and analytical precision for carbon, nitrogen and oxygen isotope analyses were 0.21‰, 0.25‰, 0.23‰, respectively.

2.4. Statistical analysis

Data were averaged for each species, and the average values for each species were analyzed for differences among growth forms. Data were tested for normality with a Shapiro–Wilk Test and all variables were found to be non-normal and were log-transformed before analysis. Raw values are reported in all figures. Comparisons of variables among growth forms were performed with one-way ANOVA in SAS ver. 9.1. Differences among growth forms were tested with a *post hoc* Duncan's multiple range test. We used dual isotope plots to evaluate groupings of species based on isotopic composition, and evaluated linear relationships, if apparent, with analysis of Pearson correlation.

3. Results

Tissue $\delta^{13}\text{C}$ values across all species ranged from a minimum of -32.7‰ in the shrub *Nissolia fruticosa* to a maximum of -12.3‰ in the C_4 grass *Brachiaria fasciculata* (table S1). The frequency distribution of isotopic values showed a bimodal distribution with a large mode at -28‰ indicating C_3 photosynthesis and a smaller mode near -15‰ suggesting CAM or C_4

photosynthesis (figure 1(a)). Tissue $\delta^{15}\text{N}$ values ranged from -8.8‰ in the epiphyte *Tillandsia schiedeana* to $+7.7\text{‰}$ in the shrub *Bunchosia swartziana*, and also showed a bimodal distribution with a large mode around $+3\text{‰}$ and a very small mode near -7‰ (figure 1(b)). Tissue N concentration varied significantly among growth forms (figure 2(a)). Epiphytes and terrestrial succulents were statistically indistinguishable varying around 1% tissue N and were significantly lower in tissue N than trees, shrubs, herbs and vines, which were statistically similar and varied around 3% (figure 2(a), $F_{1,66} = 22.90$, $p < 0.0001$). Tissue C concentration was highest in trees, shrubs and vines, intermediate in herbs and epiphytes and lowest in terrestrial succulents (figure 2(b), $F_{1,66} = 6.23$, $p < 0.015$). Mean tissue $\delta^{15}\text{N}$ across epiphytes was -4.95‰ and was significantly lower than all other growth forms which had values around $+3\text{‰}$ (figure 2(c), $F_{1,66} = 22.56$, $p < 0.0001$). Mean terrestrial succulent and epiphyte tissue $\delta^{13}\text{C}$ was around -14‰ and was similar to the herbaceous grass *Brachiaria fasciculata* (table S1), but significantly greater than means of all other growth forms, which varied between -26 and -29‰ (figure 2(d), $F_{1,66} = 44.80$, $p < 0.0001$). Mean tissue $\delta^{18}\text{O}$ varied from $+21.6\text{‰}$ in the tree *Acacia pennatula* to $+28.2\text{‰}$ in the terrestrial succulent cactus *Pterocereus gaumeri* and there were no significant differences among growth forms (figure 2(e), $F_{1,16} = 4.163$, $p = 0.058$).

A plot of $\delta^{15}\text{N}$ against $\delta^{13}\text{C}$ showed that epiphytes, terrestrial succulents and one C_4 herb were separated from all other terrestrial plants along an axis of $\delta^{13}\text{C}$, largely reflecting the difference between C_4 and CAM photosynthesis in the -12 to -15‰ range and C_3 photosynthesis in the -26 to -32‰ range (figure 3). Species within the C_4 and CAM range were further separated along an axis of $\delta^{15}\text{N}$ with negative values associated with epiphytes and positive values associated with terrestrially rooted plants.

Epiphytes had a relatively small range of approximately $+24$ to $+26\text{‰}$ $\delta^{18}\text{O}$, whereas trees ranged from $+22$ to $+25\text{‰}$ $\delta^{18}\text{O}$ and terrestrial succulents ranged from $+23$ to $+28\text{‰}$ $\delta^{18}\text{O}$ (figure 4). Values for $\delta^{18}\text{O}$ were not related with tissue $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (figures 4(a) and (b)), but there was a significant negative correlation between tissue N and $\delta^{18}\text{O}$ (figure 4(c), $r = -0.61$, $p = 0.005$).

4. Discussion

Our results indicate that stable isotopic composition of bulk photosynthetic tissue can provide information on how resources such as CO_2 and N are acquired from the environment and how patterns of acquisition differ among major growth forms. We began with an *a priori* scheme for separating species into functional groups based on whole plant morphology and found that using stable isotopes as a grouping factor to represent

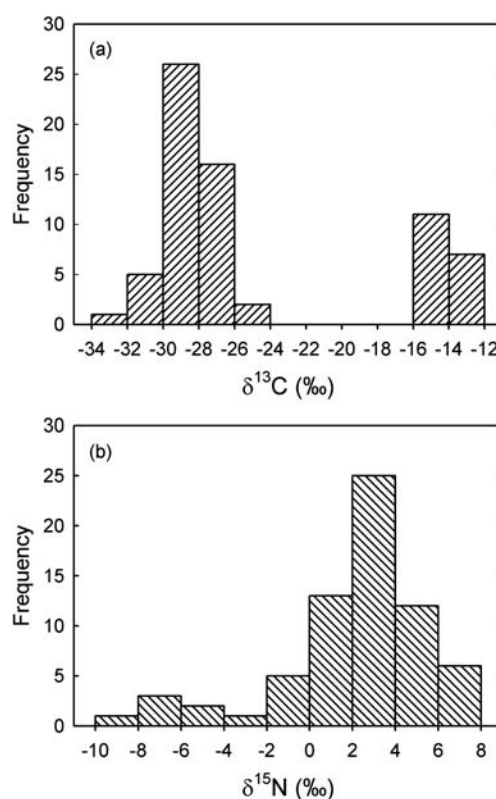


Figure 1. Frequency of (a) carbon stable isotopic composition ($\delta^{13}\text{C}$) and (b) nitrogen stable isotopic composition ($\delta^{15}\text{N}$) of photosynthetic tissue for 68 tropical dry forest plants from Dzibilchaltún National Park, Yucatan, Mexico. Each bar represents a 2‰ range of $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$.

tendencies in resource acquisition resulted in fewer groups, with similarity in rooting habitat or photosynthetic pathway structuring much of the associations. Some of the differences revealed by stable isotope analysis also reflect mechanisms for overcoming strong annual water deficit, including the presence of water saving modes of photosynthesis such as CAM and C_4 (Ehleringer and Monson 1993), as well as the possibility of diverse N sources beyond mineral soil that may vary from atmospheric N absorption by epiphytes (Hietz *et al* 2002), to biological N_2 fixation in species from Fabaceae, the legume plant family (McKey 1994, Sprent 2009). These results suggest that environmental change, including alterations of atmospheric N-deposition and changes in the seasonality or variability of precipitation, could have large impacts on the function or long-term species composition of this forest.

One of the most striking results was that in contrast to tropical wet forest, where a mix of C_3 and CAM epiphytes is possible (Silvera *et al* 2009), all epiphytes in this dry forest have CAM photosynthesis. Tropical epiphytes, especially orchids, are known to display a broad range in photosynthesis that varies from strong CAM, to C_3 , with some intermediate or weak CAM species. (Winter and Holtum 2002, Silvera *et al* 2005). There is evidence that some epiphytes can alter use of CAM and C_3 pathways throughout the year, with more CO_2 assimilated through the C_3 pathway during

the wet season than in the dry season (Goode *et al* 2010). However, the TDF at Dzibilchaltún appears too dry to support C_3 epiphytes in the canopy and the epiphyte $\delta^{13}\text{C}$ values are consistent with most of their CO_2 assimilated through the CAM pathway (Ricalde *et al* 2010). In this sense, isotopes in this TDF reflect stronger differences among growth and a more extreme commitment to resource acquisition compared to wet equatorial tropical forest.

Among C_3 plants in this study, there was also large variation in $\delta^{13}\text{C}$, with a 7‰ range among canopy trees, indicating contrasting long-term gas exchange behavior. Because leaf $\delta^{13}\text{C}$ in C_3 plants is linked to the supply of CO_2 at the site of carboxylation through photosynthesis and stomatal conductance (Farquhar and Richards 1984, Cernusak *et al* 2013), a 7‰ range suggests large variation in access to groundwater or stomatal control. In the karst soils of the Yucatan peninsula, species often differ in water-use efficiency because of differential access to underground water, which, when available, can allow tree species to extend leaf and fruit phenology (Valdez-Hernández *et al* 2010). The rapid development of deep roots appears to be an important strategy for evergreen tree species to acquire water during the dry season, whereas, in addition to losing a portion of their leaves, drought-deciduous trees minimize water loss from remaining leaves during the dry season (Hasselquist *et al* 2010). These results

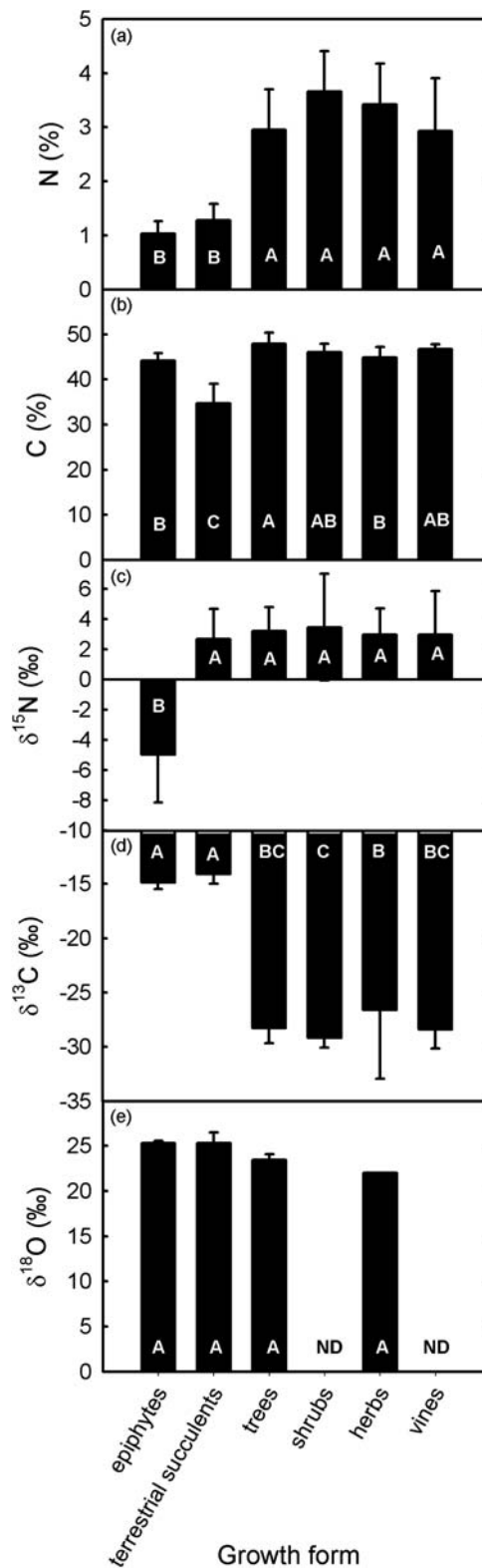


Figure 2. Mean (± 1 SD) (a) Nitrogen concentration (N), (b) carbon concentration (C), (c) nitrogen stable isotopic composition ($\delta^{15}\text{N}$), (d) carbon stable isotopic composition ($\delta^{13}\text{C}$), and (e) oxygen stable isotopic composition ($\delta^{18}\text{O}$) of photosynthetic tissue for contrasting growth forms from tropical dry forest in Dzibilchaltún National Park, Yucatan, Mexico. Results of 1 way ANOVA are presented and values with the same letter are not significantly different at an alpha of 0.05. ND indicates no data for $\delta^{18}\text{O}$ of shrubs and vines.

emphasize how water availability structures alternative strategies among tree species in this tropical dry forest.

Our results also demonstrated large variation in tissue N concentration and $\delta^{15}\text{N}$. Epiphytes had the most distinct $\delta^{15}\text{N}$ values and because they are not rooted in

mineral soil, they must obtain their N from the atmospheric sources or decaying organic matter from their host. Previous studies also report low $\delta^{15}\text{N}$ values in epiphytes (Stewart *et al* 1995, Hietz *et al* 1999), and values of $\delta^{15}\text{N}$ in NH_4^+ , NO_3^- and dissolved organic N

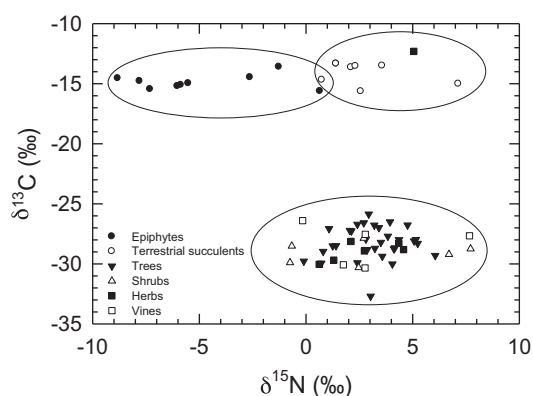


Figure 3. Dual isotope plot of carbon stable isotopic composition ($\delta^{13}\text{C}$) and nitrogen stable isotopic composition ($\delta^{15}\text{N}$) of photosynthetic tissue for 68 tropical dry forest plant species from Dzibilchaltún National Park, Yucatan, Mexico. Circled groups represent functional classifications (see text for details).

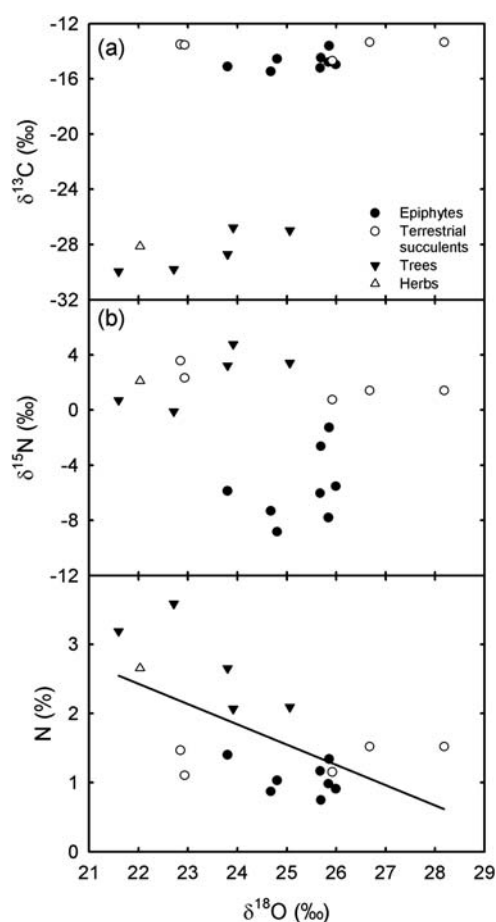


Figure 4. Dual isotope plots of (a) carbon stable isotopic composition ($\delta^{13}\text{C}$), (b) nitrogen stable isotopic composition ($\delta^{15}\text{N}$), and (c) nitrogen concentration (N) as a function of oxygen stable isotopic composition ($\delta^{18}\text{O}$) of photosynthetic tissue for 19 tropical dry forest plant species from Dzibilchaltún National Park, Yucatan, Mexico.

in precipitation in are often negative, especially in non-polluted areas (Heaton 1987, Cornell *et al* 1995, Hietz *et al* 2002). Because the epiphytes in this study have such a departure from terrestrial plant tissue, and there was little development of organic matter on branches in this TDF, it appears that they receive a large proportion of N from the atmosphere. This could facilitate CAM, which requires extra metabolic steps. Tissue N

concentration was not high for CAM epiphytes or terrestrial succulents, likely because of allocation to storage tissues for C-rich malate during the night phase. However, the atmospheric contribution of N to epiphytes is important when considering that epiphytes had similar tissue N concentrations as terrestrial succulents when apparently most or all of their N source is the atmosphere. In contrast to the low N tissue of

CAM plants, many terrestrial plants in this study had high tissue N, up to 4.66% in *Chloroleucon mangense* (table S1). This could be advantageous for increasing drawdown of intercellular CO₂ for a given stomatal conductance (Wright *et al* 2003). High tissue N concentration could also be facilitated by alternative N sources. Trees showed a large range in $\delta^{15}\text{N}$ from -0.10 to $+6.70$, and many of the lower values were from legumes, which have the possibility of developing symbiotic relationships with N₂-fixers (McKey 1994, Sprent 2009). A high N availability through accessing alternative N sources would be especially beneficial for the many dry season deciduous species in this TDF, which require nutrients to regrow a new canopy of leaves at the beginning of each wet season. Therefore, alterations in atmospheric N-deposition would increase N availability for all species and potentially reduce this advantage if leguminous trees are actively fixing N₂ at this site.

For oxygen isotopes, an *a priori* prediction is that values for C₃ plants should be higher than CAM plants because of differences in vapor pressure deficit when stomata are open (Cernusak *et al* 2008). However, we also found a large range of $\delta^{18}\text{O}$ in CAM plants, indicating that they may keep their stomates open during part of the day and incorporate some CO₂ through the C₃ pathway during the wet season. This is consistent with seasonal variation in use of C₃ and CAM pathways (Sutton *et al* 1976, Winter *et al* 1978, Goode *et al* 2010, Winter *et al* 2011), and could be an important mechanism for maximizing CO₂ uptake through both the CAM and C₃ pathways when water is available and reverting to strong CAM during the extended dry season. Epiphytes showed a smaller range, suggesting that they are more restricted in their modulation of stomatal behavior due to a more extreme lack of water. However, because we were only able to measure a subsample of our study species, further data is needed to properly distinguish stomatal behavior strategies among growth forms using $\delta^{18}\text{O}$.

5. Conclusion

Our data indicate that whereas growth forms offer a convenient way to organize the biodiversity of TDFs, other measurements such as stable isotopes, which provide patterns of resource acquisition, reveal a separation of plant species based more on process than morphology. Our data showing a diversity of water-saving modes of photosynthesis indicate that the limitations placed on photosynthetic CO₂ acquisition in this TDF are severe. The large diversity of $\delta^{15}\text{N}$ values also reveals a broad range of N acquisition patterns, much of which could be linked to maximizing CO₂ assimilation. Yet, there are still key questions that remain. First, N₂ fixation may be important because the abundance of legumes in the canopy and the high N concentration of many of the C₃ species. Second, photosynthetic capacity should be linked to leaf N concentration, and

leaf life span (Wright *et al* 2004, Maire *et al* 2015), yet whether further linkages to N₂ fixation exist is yet to be unraveled. Finally, access to water appears to vary strongly among plant species and a better understanding of how this controls annual pulses of leaf deployment and senescence is needed (Xu *et al* 2016). Overall, the diversity of stable isotopic composition of contrasting growth forms in this TDF reveal a broad range of metabolic behavior with regards to acquisition of water, carbon and nitrogen from the environment and reflect numerous mechanisms for coping with strong annual drought.

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