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Research paper

Exploiting water versus tolerating drought: water-use strategies of trees in a secondary successional tropical dry forest

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In seasonal plant communities where water availability changes dramatically both between and within seasons, understanding the mechanisms that enable plants to exploit water pulses and to survive drought periods is crucial. By measuring rates of physiological processes, we examined the trade-off between water exploitation and drought tolerance among seedlings of trees of a tropical dry forest, and identified biophysical traits most closely associated with plant water-use strategies. We also explored whether early and late secondary successional species occupy different portions of trade-off axes. As predicted, species that maintained carbon capture, hydraulic function and leaf area at higher plant water deficits during drought had low photosynthetic rates, xylem hydraulic conductivity and growth rate under non-limiting water supply. Drought tolerance was associated with more dense leaf, stem and root tissues, whereas rapid resource acquisition was associated with greater stem water storage, larger vessel diameter and larger leaf area per mass invested. We offer evidence that the water exploitation versus drought tolerance trade-off drives species differentiation in the ability of tropical dry forest trees to deal with alternating water-drought pulses. However, we detected no evidence of strong functional differentiation between early and late successional species along the proposed trade-off axes, suggesting that the environmental gradient of water availability across secondary successional habitats in the dry tropics does not filter out physiological strategies of water use among species, at least at the seedling stage.

Keywords: carbon capture, drought tolerance, exploitation capacity, hydraulic conductivity, resistance to embolisms, trade-off.

Introduction

Among plant species, physiological trade-offs are driven by limitations on resource availability, which restricts resource allocation among major functions (Reich 2014), thereby affecting species ecological performance and distribution (Kneitel and Chase 2004). A general trade-off has been detected between species' capacity to exploit and compete for resources when they are abundant, and the ability to survive under low resource availability (fast–slow growth trade-off) (Grime 1977, Poorter and Bongers 2006, Reich 2014). This trade-off has recently been proposed as a template for representing solutions for coping with variation in multiple resources such as light, nutrients or water (Reich 2014). Specifically, the water exploitation versus drought tolerance trade-off expresses the conflict between increasing the capacity for water uptake and use, and the ability to conserve water and tolerate soil and tissue desiccation. Tolerance involves traits that enable the plant to continue functioning in spite of low soil and plant water potentials (Larcher 2003, Tyree et al. 2003). It is thought that expression of traits conferring tolerance requires a high proportion of the resources captured by the plant, thereby restricting allocation to other structures that could potentially maximize resource capture and growth (Grime and Hunt 1975, Chapin et al. 1993, Ryser 1996, Aerts 1999, Grime 2001, Freschet et al. 2010, Reich 2014).

Conflicts between water exploitation and drought tolerance have been inferred from negative correlations between two functions operating at the same scale, but rarely from correlations between physiological rates as evaluated during responses to actual drought. This is the case with the classical xylem efficiency and safety trade-off, wherein hydraulic conductivity and vulnerability to embolism are measured on excised branches from plants that were not subjected to drought (Jacobsen et al. 2007, Markesteijn et al. 2011*a*). Furthermore, results from these evaluations are normally extrapolated to the organismal level, without taking into account that coordination of other traits and processes could mitigate the effects of drought at the organismal level (Meinzer et al. 2008, 2010). For example, a species with xylem that is highly efficient and vulnerable to embolism may not be subject to risk of rapid hydraulic failure during a period of soil drought if it has deep roots (Paz 2003, Poorter and Markesteijn 2008, Hasselquist et al. 2010, Fortunel et al. 2012, Pérez-Ramos et al. 2013, Paz et al. 2015), reduces its leaf area (Bucci et al. 2005) or uses water reserves in stems (Borchert 1994, Scholz et al. 2011, Pineda-García et al. 2013, Wolfe and Kursar 2015). Thus, an evaluation of rates of physiological processes involved in the water exploitation–drought tolerance trade-off may be better understood when measuring the integrated response of plants and when plants are tested under both conditions of water availability and drought, a task infrequently done (Meinzer et al. 2010). Additionally, although some biophysical traits such as wood and leaf density have been associated with physiological tolerance to drought (Hacke et al. 2001, Jacobsen et al. 2007, Kursar et al. 2009, Markesteijn et al. 2011*a*, Méndez-Alonzo et al. 2012), understanding of mechanistic linkages between simple biophysical traits and higher order traits is still limited.

In seasonal plant communities such as tropical dry forests, the limited time for plant growth is defined by the length of the rainy season and also by the frequency and length of recurrent dry spells during this period (Lott et al. 1987, García-Oliva et al. 1991, de Mattos et al. 2002, Peña and Douglas 2002, Engelbrecht et al. 2006, Páramo-Pérez 2009). Under these conditions, plant species could increase their fitness by rapidly maximizing their capacity for water uptake and growth during periods with abundant rain, and also by tolerating water deficits during short rainy season dry spells or at the beginning of the dry season (Pineda-García et al. 2011, Méndez-Alonzo et al. 2012). Additionally, large variation in the risk of drought has been observed along gradients of secondary succession in tropical dry forests. Early successional stages experience higher loads of direct radiation, making the air warmer with lower air humidity and reduced water content in the top soil (10 cm depth), compared with late successional stages (Lebrija-Trejo et al. 2011, Pineda-García et al. 2013), and the risk could be magnified with the onset of the dry season and by the short-dry spells (García-Oliva et al. 1991, Páramo-Pérez 2009). Other resources may vary at the secondary succession, although the lack of variation in soil fertility associated with the secondary succession reported in a tropical dry forest region (Sandoval et al. 2009) suggests that at the top soil, water is one of the major resources dictating seedlings' community organization. This contrasting water availability scenario could promote differentiation in water-use strategies among species along the secondary succession.

In this study, we selected 12 species differing in their distribution along a gradient of drought risk corresponding to different stages of secondary succession in a tropical dry forest. We sought to document whether the water exploitation–drought tolerance trade-off is expressed when measuring the rates of physiological processes of seedlings subjected to contrasting water availability scenarios. To do so, we characterized species water-use strategies based on water transport capacity, supply and use in leaves, as well as growth rates attained under non-limiting water supply. Second, we quantified changes in plant water status and rates of physiological processes during a period of experimentally imposed soil drying that simulated the rate of soil drying during the beginning of the dry season or during a dry spell. Additionally, we measured above and below ground biophysical traits under non-limiting water supply to identify the traits most closely associated with physiological performance under the two water availability scenarios described above.

Materials and methods

Study system

The study was conducted with seedlings of the most common tree species in the tropical dry forest region of Chamela, Jalisco on the Pacific coast of Mexico (19°30′N, 105°03′W). Mean annual precipitation in the region is 748 mm, most of which falls from July to October, with a marked dry season during the rest of the year (Lott et al. 1987). At Chamela, most tree species drop their leaves in response to the seasonal drought, remain leafless for 8 months and produce new leaves with the onset of the rainy season (Bullock and Solis-Magallanes 1990). However, the timing of leaf abscission differs widely between species (Méndez-Alonzo et al. 2012). The landscape around Chamela is a mosaic of patches ranging from mature forest to areas of secondary vegetation with different recovery times following abandonment of human activities. In this landscape, the vegetation in permanent plots across a chronosequence from 0 to 12 years after abandonment plus mature forest has been censused for more than 6 years (Maza-Villalobos et al. 2011, Ramos-López 2012). Based on long-term vegetation data of secondary succession (Maza-Villalobos et al. 2011, Ramos-López 2012), we selected 12 tree species differing in their successional status (Table 1) to study plant physiological performance during drought and under non-water-limited conditions. As adults, all

Table 1. Study species representative of early and late successional sites in the tropical dry forest of Chamela, Mexico. Note: early successional species are those specialized at colonizing early secondary sites, plus those species that successfully establish in early stages but are also abundant at the late successional stages. Late successional species are those species mostly restricted to late successional to old growth forest sites.

Early successional species	Late successional species
Mimosa arenosa (Willd.) Poir.	*Caesalpinia coriaria* (Jacq.) Willd.
Senna atomaria (L.) H.S. Irwin & Barneby	*Lonchocarpus constrictus* Pittier
Piptadenia constricta (Micheli & Rose ex Micheli) J.F. Macbr.	*Ipomea wolcottiana* Rose
Caesalpinia eriostachys Benth.	*Apoplanesia paniculata* C. Presl
Cordia eleagnoides DC	*Ceiba grandiflora* Rose
Gliricidia sepium (Jacq.) Kunth ex Walp.	*Ceiba aesculifolia* (H.B.K.) Britton & Baker

the species selected drop their leaves during seasonal drought. Because we were interested in discerning traits that enable or impede establishment and persistence in the early successional sites, we selected two groups of six species each: (i) 'early successional species', comprising specialists (pioneers) largely restricted to early successional stages, plus generalists that appear during early stages of succession, but also remain abundant across different successional stages and (ii) 'late successional species', comprising taxa that successfully establish in late to old-growth forest, but not in recently abandoned sites (Table 1).

Experimental design

Seeds from at least 10 trees of each of the 12 species were collected during the peak of fruiting. Seeds from the early successional species were harvested exclusively from trees growing in early successional sites and seeds from late successional species were collected in late successional and mature forest sites. To evaluate physiological responses to soil drought and water-use strategies prior to the imposition of drought, we conducted an experiment on 1-year-old seedlings under controlled conditions in a greenhouse. Seeds were placed in silica sand beds for germination in the greenhouse. Fifteen days after radicle emergence, and with the first pair of leaves completely expanded, 56 seedlings per species were randomly selected and transplanted to ~6.0 l pots (14 cm diameter × 40 cm tall) with basal drainage containing silica river-sand from a tropical dry forest area (one seedling per pot). Concurrently, we collected an additional 10 seedlings per species to quantify the initial biomass, which was used to calculate the relative growth rate (RGR) (see below). Initially, each pot received a dose of controlled-release fertilizer (14.61 g of Multicote 8: 18N–6P–12K + 2MgO + ME; Haifa Chemicals, Israel). Pot positions were assigned in a randomized block design to statistically control for solar radiation and temperature variation in the greenhouse. Plants were grown for a 12-month period at low soil water deficit (soil water potential between –0.05 and –0.22 MPa). The average greenhouse conditions were: air temperature 21.5 °C (48–7.6 °C), relative humidity 60% (85–41%) and a daily average photosynthetic photon flux of 745 μmol m^{-2} s^{-1} (max 917 μmol m^{-2} s^{-1}). At 12 months, six blocks, containing ~10 plants per species, were subjected to progressive soil desiccation by cessation of watering.

Physiological and biophysical traits under non-limiting water supply

Before experimental soil drought was imposed, we characterized physiological and biophysical traits at the leaf, stem and root level. The maximum photosynthetic rate (A_{max}) of four seedlings of each species was measured between 08:00 and 11:00 h in two healthy, fully expanded leaves with a portable infrared gas analyzer (Li-Cor 6400, LI-COR, Lincoln, NE, USA). The CO_2 concentration and the photosynthetically active radiation were kept at ~400 μmol mol^{-1} and 1500 μmol m^{-2} s^{-1}, respectively. The stem hydraulic conductivity was determined on five seedlings per species. The stem of each seedling was collected before dawn and it was cut at the base under water, to reduce at maximum any possibility of xylem blockage during sample manipulation. The sample was immediately transported to the laboratory where a second cut was made underwater with a razor blade to remove possible vessel obstructions. Leaves were removed from these 10 to 14-cm-long stem sections and the leaf scars were sealed with Parafilm. Each stem section was connected to a water reservoir containing a degassed and filtered (0.2 μm) 10 mM KCl solution positioned at a height sufficient to generate a pressure head of ~3 kPa. With the stem section connected to the reservoir and after a 15 min period of stabilization, we measured the mass flow (g s^{-1}) through the section. We recorded three consecutive measurements to assure that the flow had stabilized. Hydraulic conductivity (k_h) was calculated as the ratio between the water flux (F) passing through the stem section and the pressure gradient (dP/dx) (Tyree and Ewers 1991). The total length and the diameter of the section were measured to 0.01 mm. The stem-specific hydraulic conductivity (k_s) sensu Tyree and Ewers (1991) was calculated as $k_s = (k_h$/stem xylem cross-sectional area) (Table 2). Additionally, we quantified the wood density (Wd; g cm^{-3}) and water content (SWC; %) for each stem section following Pineda-García et al. (2011).

Xylem anatomical traits were determined from the same stem sections used in the hydraulic conductivity determinations. Stem samples 0.5 cm long were fixed with formalin–acetic acid–alcohol, dehydrated in a series of ethanol, up to 100%, transferred to propylene oxide and embedded in epoxy resin. Transverse sections of the xylem were made with a sliding microtome, using a metal knife. Sections were collected in a Petri dish in 70% ethanol, stained with 0.01% aqueous safranin and mounted in synthetic resin. A digital photograph was taken for each section

Table 2. Biophysical and physiological traits determined for each of the 12 dry forest species; abbreviations, derivations and units are shown.

Trait		Formula	Units
RGR	Relative growth rate	ln(initial biomass) − ln(final biomass)/(days)	g g^{-1} $days^{-1}$
LDMC	Leaf dry matter content	Leaf dry weight/leaf fresh weight	g g^{-1}
SLA	Specific leaf area	Leaf area/leaf dry weight	cm^2 g^{-1}
A_{max}	Maximum photosynthetic rate		µmol g^{-1} s^{-1}
Wd	Wood density	Xylem dry weight/xylem volume	g cm^{-3}
SWC	Stem water content	(Xylem fresh weight − dry weight)/dry weight	%
k_s	Stem-specific hydraulic conductivity	(K_h/xylem cross-sectional area) × xylem length	mmol m^{-1} s^{-1} MPa^{-1}
D_h	Hydraulic weighted diameter	D_h:[(1/n) $\sum d^4$]$^{1/4}$	mm
VD	Vessel density	Number of vessels/area	mm^2
SRL	Specific root length (<2 mm)	Length of the thin roots/dry weight	cm g^{-1}
RDMC	Root dry matter content (>2 mm)	Root dry weight/root fresh weight	g g^{-1}

with a light microscope (Fisher Scientific Micromaster, USA). For each section, an image obtained with the 10× objective was used to estimate the vessel density (VD; number of vessels mm^{-2}). At the same time, images of vessels were obtained under the 40× objective until a total of 40 vessels were photographed. For each vessel, we quantified the maximum and minimum diameter by using ImageJ software (National Institutes of Health, Bethesda, MD, USA, http://rsb.info.nih.gov/ij/). The hydraulic weighted diameter was obtained as:

$$D_h : \left(\frac{1}{n}\sum d^4\right)^{1/4},$$

where d is the vessel diameter that represents the average of the maximum and minimum diameter of each vessel, and n is the number of vessels in that section (Poorter et al. 2010).

We calculated the average specific leaf area (SLA; cm^2 g^{-1}) from three fully expanded, healthy leaves for each seedling, as the ratio of leaf lamina area (excluding petiole) : leaf dry mass, and also the leaf dry matter content (LDMC; g g^{-1}) as the ratio between the leaf dry weight and the leaf fresh weight. The entire root system of each seedling was carefully extracted and washed with water to remove any soil particles. The root system was divided into two diameter classes: fine or absorption roots (≤2 mm) and thick or storage roots (>2 mm). The total length of fine roots was quantified from 400 dpi resolution images obtained with a double-lamp scanner (Epson 10000XL, Epson America Inc., Long Beach, CA, USA) and analyzed with WinRhizo (Regent Instruments, Inc., Neplean, ON, Canada). For the thick roots we obtained the fresh weight. The roots from both categories were oven-dried for 72 h at 70 °C. Afterwards, roots were weighed to 0.0001 g with a balance. The specific root length (SRL; cm g^{-1}) of fine roots was derived as the ratio between the fine root total length and the dry weight. The dry matter content of thick roots (RDMC; g g^{-1}), analogous to the leaf dry matter content, was calculated as the dry mass of the thick roots divided by their fresh mass. Finally, RGR (g g^{-1} day^{-1}) was estimated as RGR = ln(plant initial biomass) − ln(plant final biomass)/(days) (Table 2).

Physiological traits during experimental soil desiccation

Photosynthetic CO_2 assimilation rates (A) were monitored on 26 randomly selected seedlings of each species during the desiccation trial. The measurement protocol was the same as that used under non-limiting water supply. For a complete description of the measurement protocols, see Pineda-García et al. (2013). The photosynthetic rate was transformed to percentage loss (PLA) relative to the maximum value registered before the beginning of the experimental drought by applying the formula: PLA = 100 × ((A_{max} − A)/A_{max}). The same group of plants was used for monitoring percentage loss of initial leaf area (as a measurement of the degree of deciduousness) (PLLA) by applying PLLA = 100 × ((LA_{ini} − LA)/LA_{ini}). The percentage loss at any census was visually assessed by comparing the living leaf area to a photograph of the initial condition. The total number of censuses of both variables ranged between 10 and 50, depending on the species. All measurements were done on a daily basis, the seedling visible wilting stage was the criteria to decide when measurement should be done. Plant water status and stem hydraulic conductivity were monitored during the desiccation trial by collecting plants representing a wide range of visible wilting conditions. Sample sizes ranged from 8 to 20 depending on the species. Each plant was collected at predawn for measuring leaf water content, leaf water potential (Ψ_L) and stem k_s. Before the hydraulic conductivity determinations and to obtain leaf water content, one leaf was excised and used to extract one disc of 1 cm^2 that was immediately weighed and then oven-dried for 42 h at 70 °C. A second leaf or a distal shoot tip (depending on the species) was then immediately excised and used for Ψ_L measurements using a pressure chamber. Finally, plants were cut under water at the stem base and kept submerged inside a black plastic bag for laboratory measurements of stem k_s a few minutes later. The main stem was recut under water and used for measuring k_s, following the procedure described previously. After this, the maximum conductivity ($k_{s\,max}$) of each stem was then obtained after flushing out emboli by applying a 100 kPa pressure head during 10 min, and re-measuring water flow. For each stem, we quantified the percentage loss of hydraulic conductivity (PLC) as: PLC = 100 ×

$((k_{s\ max} - k_s)/k_{s\ max})$. We also tracked plant water status in those seedlings used for monitoring photosynthesis and leaf area loss, by inferring water potential from leaf water content. At every census, 1 cm^2 leaf disc was collected between 08:00 and 11:00 h, immediately wrapped in aluminum foil, bagged and a few minutes later processed using the protocols previously described for obtaining leaf water content. Leaf samples were always taken from the least wilted tissues available in each plant. The data obtained by destructive sampling prior to stem hydraulic conductivity determination were used to derive relationships between Ψ_L and leaf water content for each species.

Statistical analysis

The drought tolerance of each species was determined by plotting the percentage loss of the physiological functions (photosynthesis (PL*A*), leaf area (PLLA) and hydraulic conductivity (PLC) during drought against absolute values of plant water potential, by using a nonlinear, four-parameter Weibull model. To characterize the species tolerance, we derived a threshold of absolute value of Ψ_{plant} corresponding to 80% loss of each of the physiological functions (PL*A* $\Psi_{plant80}$, PLLA $\Psi_{plant80}$ and PLC $\Psi_{plant80}$). We used the Ψ_{plant} corresponding to 80% loss of function, to explore the variation in the physiological performance of the different species at extreme drought conditions. For *C. grandiflora* Rose we used the Ψ_{plant} of the 50% loss of hydraulic conductivity (PLC) instead of the PLC $\Psi_{plant80}$ because it never reached that level of cavitation. For methodological details and physiological loss data, see Pineda-García et al. (2013). In addition, for those physiological rates evaluated under non-limiting water supply (k_s, A_{max}, RGR), we calculated the mean value per species. To examine the variation of functional strategies, we took into consideration the covariation of all the physiological traits at both water availability scenarios and the tolerance–exploitation trade-off was explored by using principal component analysis (PCA). The PCA included thresholds at 80% loss of photosynthesis (PL*A*), leaf area (PLLA) and stem hydraulic conductivity (PLC), and the physiological rates observed under non-limiting water supply (k_s, A_{max}, RGR). To test for significant differences in water-use strategies between successional groups, a *t*-test was carried out on the species scores of the first PCA axis. Finally, to explore which biophysical traits were related to physiological trade-offs, we tested Pearson correlations between the PCA axis scores and morphological traits.

Results

Physiological strategy under non-limiting water supply and during soil drought

The first two PCA axes explained a total of 82.8% of the variation (Figure 1). The first axis explained close to 60% and summarized variation between maximizing water transport, carbon gain and RGR, versus tolerating drought. For example, species

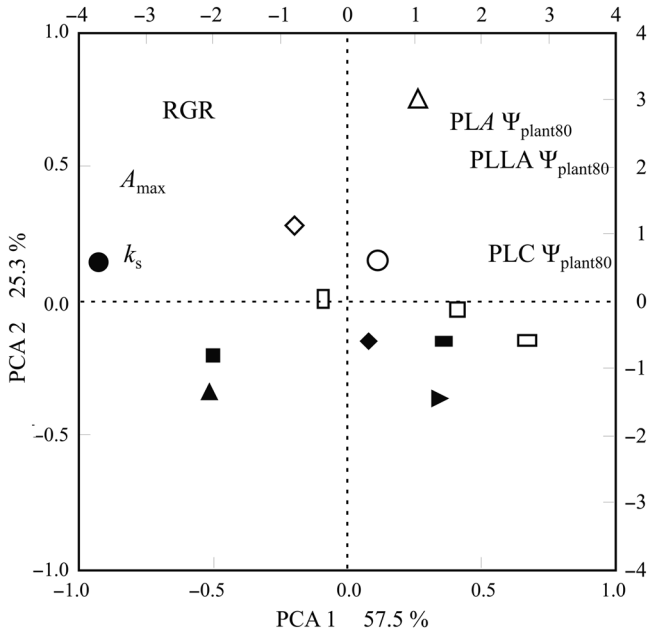

Figure 1. Principal component analysis showing the resource exploitation capacity–drought tolerance trade-off among tropical dry forest species. The analysis included the stem-specific hydraulic conductivity (k_s), maximum photosynthetic rate (A_{max}) and RGR which were measured under non-limiting water supply, and also the plant water potentials (Ψ_{plant}) at which 80% of the photosynthetic rate (PL*A*), leaf area (PLLA) and stem hydraulic conductivity (PLC) were lost. Closed symbols represent late secondary successional species and open symbols early secondary successional species. *Caesalpinia eriostachys* (open square), *C. eleagnoides* (open diamond), *G. sepium* (open triangle), *S. atomaria* (open vertical rectangle), *P. constricta* (open horizontal rectangle), *M. arenosa* (open circle), *A. paniculata* (filled diamond), *C. coriaria* (filled horizontal rectangle), *C. aesculifolia* (filled circle), *C. grandiflora* (filled triangle), *I. wolcottiana* (filled square), *L. constrictus* (filled right sided triangle).

with a high stem hydraulic specific conductivity (k_s, vector loading: −0.80), photosynthetic capacity (A_{max}: −0.75) and RGR (RGR: −0.62) were at the negative side of the first axis, resulting in a high water exploitation capacity overall. In contrast, those species exhibiting high tolerance to drought at the stem and leaf levels (PLC: 0.93, PLLA: 0.76 and PL*A*: 0.61) were at the positive side of the first axis. It is important to note that in this analysis threshold values for PL*A*, PLLA and PLC were expressed as absolute values. Thus higher values imply loss of function (photosynthesis, leaf area and xylem conductivity) at more negative water potentials. On the other hand, the second axis was represented by the components associated with leaf photosynthesis during drought and with the RGR. Species capable of realizing high growth rates under no water limitation, also lost 80% of the photosynthetic rate at more negative plant water potentials.

Water-use strategy between successional groups

A *t*-test on the PCA 1 axis indicated that successional groups did not differ along the water exploitation–drought tolerance trade-off ($t = -1.5$, $P = 0.15$).

Table 3. Pairwise correlation matrix of biophysical and physiological traits under high water availability, physiological responses during soil desiccation, and the two axes of the PCA that reflected the exploitation–tolerance trade-off. The pairwise correlations were explored with the mean value of each trait for each of the 12 species. The table shows the Pearson correlations coefficient (r) and in italics are the significant correlations.

	SLA ($cm^2\ g^{-1}$)		LDMC ($g\ g^{-1}$)		Wd ($g\ cm^{-3}$)		SWC (%)		D_h (mm)		VD (mm^2)		SRL ($cm\ g^{-1}$)		RDMC ($g\ g^{-1}$)	
	r	P	r	P	r	P	r	P	r	P	r	P	r	P	r	P
A_{max} ($\mu mol\ g^{-1}\ s^{-1}$)	0.68	*0.01*	−0.58	*0.05*	−0.63	*0.03*	0.56	0.06	0.76	*0.004*	−0.81	*0.001*	0.19	0.56	−0.57	*0.05*
k_s ($mmol\ m^{-1}\ s^{-1}\ MPa^{-1}$)	0.51	0.09	−0.47	0.12	−0.48	0.12	0.58	*0.05*	0.79	*0.002*	−0.44	0.15	−0.13	0.70	−0.55	0.06
RGR ($g\ g^{-1}\ days^{-1}$)	0.75	*0.005*	−0.78	*0.003*	−0.58	*0.05*	0.66	*0.02*	0.81	*0.001*	−0.76	*0.004*	−0.25	0.43	−0.57	*0.05*
PLA $\Psi_{plant80}$ (MPa)	−0.02	0.95	0.02	0.94	0.28	0.38	−0.26	0.41	−0.41	0.19	0.11	0.73	−0.55	0.06	0.30	0.34
PLC $\Psi_{plant80}$ (MPa)	−0.45	0.14	0.52	0.08	0.72	*0.008*	−0.69	*0.01*	−0.81	*0.001*	0.70	*0.01*	−0.42	0.18	0.74	*0.006*
PLLA $\Psi_{plant80}$ (MPa)	−0.15	0.65	0.27	0.39	0.66	*0.02*	−0.62	*0.03*	−0.59	*0.04*	0.38	0.23	−0.21	0.51	0.67	*0.02*
PCA 1	−0.56	0.06	0.58	*0.05*	0.75	*0.005*	−0.75	*0.005*	−0.92	*<0.0001*	0.72	*0.008*	−0.22	0.48	0.77	*0.004*
PCA 2	−0.44	0.15	0.37	0.24	0	1	−0.05	0.88	−0.12	0.7	0.31	0.33	0.46	0.13	−0.03	0.93

Relationships between physiological strategy and plant biophysical traits

Pairwise correlations detected several patterns of association between stem and root biophysical traits and the physiological water-use strategies. Wood density, leaf and root dry matter content and vessel density were positively related with the PCA 1 axis scores (Table 3; Figure 2a and b). Meanwhile, the hydraulically weighted diameter, the stem water content and to a lesser degree the SLA were negatively associated with the first PCA 1 axis (Table 3; Figure 2c and d). In other words, the capacity to tolerate soil drought was associated with dense tissues, while the exploitation strategy was positively related to two xylem features; large mean diameter vessels and high capacity to store water, as well as to large SLA. Nevertheless, no relationship was found between the second PCA axis and any of the traits (Table 3).

Discussion

It has been hypothesized that drought-tolerant species are less efficient at capturing resources and growing when water is available, which results from the costs associated with the development of traits that confer tolerance (Chapin et al. 1993, Reich 2014). Results of previous studies based on correlations between stem and leaf biophysical traits are consistent with the existence of this trade-off among tropical dry forest species (Lebrija-Trejos et al. 2010, Poorter et al. 2010, Markesteijn et al. 2011*a*, Méndez-Alonzo et al. 2012). In the present study, the experimental evaluation of the coordinated physiological performance of leaves and stems both under high water supply and during soil desiccation allowed for a better understanding of the tolerance–exploitation trade-off and the ability of plants to deal with pulses of water and dry spells commonly occurring in tropical dry forests.

The species with high water transport capacity and high rates of carbon gain attained higher growth rates, but were very sensitive to soil desiccation because they shed their leaves and lost carbon gaining capacity and hydraulic conductivity at more negative plant water potentials. In contrast, the drought tolerance strategy was expressed as high resistance of stem xylem to cavitation, and greater ability to maintain leaf and stem function at higher levels of plant water deficit, but at the cost of low rates of photosynthesis and growth when water is available. Previous studies have focused on the functional conflict between xylem efficiency and safety as evidence for the exploitation versus tolerance trade-off (Sobrado 1993, 1997, Martínez-Vilalta et al. 2002, Hacke et al. 2006, 2009, Markesteijn et al. 2011*b*, Méndez-Alonzo et al. 2012). Consistent with these studies, in our study a xylem efficiency versus safety trade-off was evident given the high loadings of both k_s under non-limited water supply and xylem vulnerability to embolism (PLC) in the first axis of the PCA analyses. However, in contrast to other studies suggesting a

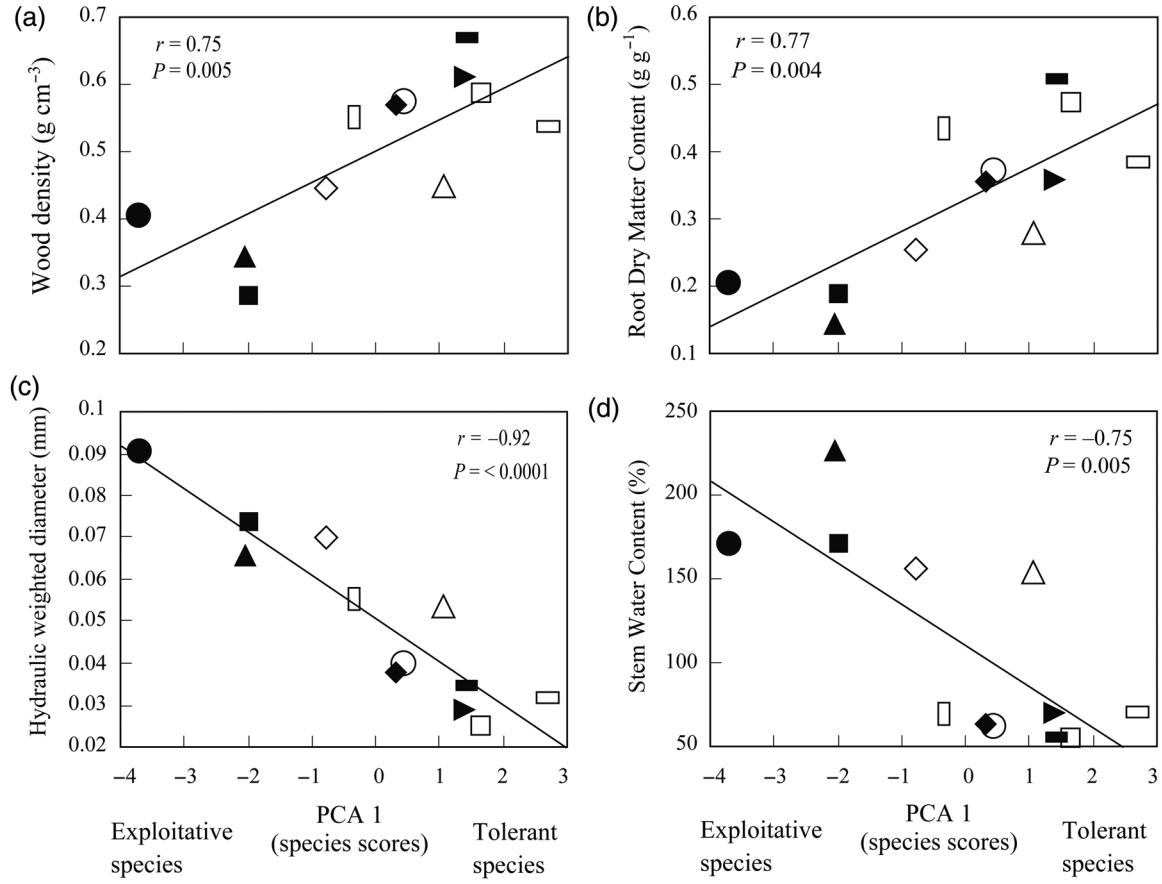

Figure 2. Relationships between biophysical traits and the resource exploitation–drought tolerance strategy among species as reflected by the species scores of the first PCA axis applied to physiological responses in the absence and presence of water limitation (see Materials and methods). Wood density (a), root dry matter content (b), hydraulically weighted vessel diameter (c) and stem water content (d). Species symbols as in Figure 1.

weak or no coordination between stem and leaf economies (Chen et al. 2009, Baraloto et al. 2010), in our data set, leaf-level physiology was coordinated with xylem function, both under non-water-limited and drought conditions. Together, our results suggest that the conflict between exploiting water and tolerating drought is likely one of the primary components of a more general trade-off between high rates of resource exploitation and growth, versus high resource-use efficiency but at a reduced growth rate (Reich 2014). Thus, exploitative species with high water demands for leaf carbon gain require high xylem water transport capacity and overall, both traits promote growth (Brodribb and Feild 2000, Santiago et al. 2004). However, sustaining high water transport rates requires vessels with larger lumen diameter and thinner walls. Consequently, structural reinforcement that prevents cavitation or implosion (thick vessel and fiber walls) is less developed, reducing plant tolerance to drought (Hacke et al. 2001). Although drought-tolerant species are able to maintain stem hydraulic conductivity and retain leaves at lower plant water potentials, when water is available they have a restricted capacity for water and carbon acquisition. In our study, drought-tolerant species showed low RGRs, likely resulting from a combined effect of the reduced capacity for water transport and carbon acquisition, and also from reduced carbon allocation to the production of new leaf area compared with the species with higher maximum rates of water consumption.

Strikingly, in our data set we detected that part of the variation in drought tolerance of leaf tissues and potential growth rate was independent of the variation of xylem drought tolerance, as indicated by the high loadings of RGR and PLA on the second axis of the multivariate analyses. This implies that in tropical dry forests, some tree species are capable of sustaining leaf functioning even when water supply is restricted by drought and also of attaining high growth rates when water is available. In other words, some species have water-use strategies that seem not to be constrained by the proposed water exploitation–drought tolerance trade-off. In our data set, this pattern is driven mostly by those nitrogen (N)-fixing legumes that may enhance photosynthetic rates through elevated enzyme activity even at low Ψ_L (see Powers and Tiffin 2010). For example, *G. sepium* and *M. arenosa* the two N fixers among our study species, lost 80% of photosynthesis at the lowest plant water potentials and also had high maximum rates of photosynthesis and growth under non-water limitation. The occurrence of this strategy (high drought tolerance and high potential growth rate) has been

mentioned in other comparative studies of trees from the dry tropics (Powers and Tiffin 2010). We hypothesize that N-fixing legumes mark a shift to high water-use efficiency along the general exploitation versus tolerance trade-off in the community. However, testing this hypothesis requires comparison of larger groups of N fixers and non-fixers.

In our study, we were also interested in exploring the importance of the exploitation–drought tolerance trade-off as a mechanism promoting species niche differentiation across the secondary succession of the tropical dry forests. However, our results did not support such a prediction, since successional groups did not differ in their water-use strategy, suggesting that a variety of strategies might be successful at every stage of the secondary succession. Future exploration needs to focus on other mechanisms such as rooting depth (Paz et al. 2015), which seems to play an important role on habitat partitioning during secondary succession.

We observed that rates of physiological processes during drought and under high soil water content were strongly associated with some tissue-level biophysical traits. The exploitation strategy was tightly associated with larger vessel hydraulically weighted diameter and higher stem water content. The relationship between stem hydraulic conductivity and the hydraulically weighted vessel diameter is direct (Tyree and Zimmermann 2002). Associations with the stem water content might reflect on one hand that greater xylem capacitance buffers tension, reducing the risk of hydraulic failure (Meinzer et al. 2008), and on the other hand that large diameter vessels tend to be associated with species having large amounts of water storage in parenchyma tissue (Méndez-Alonzo et al. 2012). Rapid resource exploitation was likewise related to high SLA. Large SLA translates into large carbon capture area per unit of biomass invested in leaf construction, which results in a higher growth capacity (Reich et al. 1998, 1999, Wright and Westoby 2000).

On the other hand, the drought-tolerant strategy was associated with high tissue densities (leaf, stem and roots). Leaf density has been associated with the plant resistance to soil drought (Niinemets 2001, Markesteijn et al. 2011*a*, Méndez-Alonzo et al. 2012). High leaf density implies small, more numerous mesophyll cells with thick walls, which makes them more resistant to collapse during drought and increases their modulus of elasticity (Niinemets 2001). A large modulus of elasticity allows for a greater change in Ψ_L with small reductions in water content (Niinemets 2001), thereby maintaining the driving force for soil water uptake and prolonging leaf carbon capture. Dense xylem is more resistant to collapse when tension is high during soil drought because it is constructed with thick-walled vessels and fibers (Hacke et al. 2001, Jacobsen et al. 2007). In our study, we found a positive association between wood density and xylem vessel wall thickness, as well as a negative association with the hydraulic diameter (data not shown), suggesting various mechanisms linking dense tissues to hydraulic safety. We found that dense roots were coordinated with dense stem and leaf tissues, suggesting that common mechanisms of drought tolerance may be operating at the root, leaf and stem levels. Overall, this pattern reflects structural coordination among plant organs (but see Fortunel et al. 2012), which was related to drought tolerance among tropical dry forest species.

Conclusions

Our work highlights the importance of evaluating whole-plant performance under contrasting water availability scenarios to gain a more dynamic perspective of plant water-use strategies. By using this experimental approach, we found that more drought-tolerant species had a limited capacity for resource capture. Although we detected wide variation in drought tolerance and in the capacity for water exploitation, neither strategy was exclusive for guilds inhabiting the extremes along the secondary succession. Future exploration needs to focus on other mechanisms such as rooting depth that could have a larger contribution to habitat partitioning along gradients of drought risk.

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Conflict of interest

None declared.

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