COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Drought response strategies of deciduous and evergreen woody species in a seasonally dry neotropical forest

Bruno Cruz de Souza[1] · Ellen Cristina Dantas Carvalho[1] · Rafael S. Oliveira[2] · Francisca Soares de Araujo[3] · André Luiz Alves de Lima[4] · Maria Jesus Nogueira Rodal[5]

Abstract

Deciduous and evergreen trees are usually considered the main coexisting functional groups in seasonally dry tropical forests (SDTF). We compared leaf and stem traits of 22 woody species in the Brazilian Caatinga to investigate whether deciduous (DC) and evergreen (EV) species have divergent water-use strategies. Our hypothesis was that DC trees compensate for their short leaf longevity by being less conservative in water use and showing higher variation in the seasonal water potential after leaf shedding. Evergreen species should exhibit a highly conservative water use strategy, which reduces variations in seasonal water potential and the negative effects of desiccation. Our leaf dynamics results indicate that the crown area of DC trees is more sensitive to air and soil drought, whereas EV trees are only sensitive to soil drought. Deciduous species exhibit differences in a set of leaf traits confirming their acquisitive strategy, which contrasts with evergreen species. However, when stomatal traits are considered, we found that DC and EV have similar stomatal regulation strategies (partially isohydric). We also found divergent physiological strategies within DC. For high wood density DC, the xylem water potential (Ψ_{xylem}) continued to drop during the dry season. We also found a negative linear relationship between leaf life span (LL) and the transpiration rate per unit of hydraulic conductivity (Λ), indicating that species with high LL are less vulnerable to hydraulic conductivity loss than early-deciduous species. Collectively, our results indicate divergence in the physiology of deciduous species, which suggests that categorizing species based solely on their leaf phenology may be an oversimplification.

Introduction

Several global climate change models (GCMs) project significant changes in temperature and rainfall for the next 85 years in many tropical regions (Intergovernmental Panel on Climate Change IPCC 2015). The seasonally dry tropical forest (SDTF) that occurs in the semi-arid region of northeastern of Brazil is especially vulnerable to climate change.

✉ Bruno Cruz de Souza
brunoecologo@gmail.com

✉ Rafael S. Oliveira
rafaelso@unicampbr

✉ Maria Jesus Nogueira Rodal
mrodal@terrra.com.br

1 Graduate Program in Ecology and Natural Resources, Science Center, Department of Biology, Federal University of Ceará - UFC, Fortaleza 60440-900, Brazil

2 Department of Plant Biology, Institute of Biology, University of Campinas, Campinas 13083-970, Brazil

3 Department of Biology, Federal University of Ceará - UFC, Fortaleza 60455-760, Brazil

4 Federal Rural University of Pernambuco, Campus of Serra Talhada, Serra Talhada 56909-535, Brazil

5 Department of Biology, Federal Rural University of Pernambuco, Botany Sector, Recife 52171-900, Brazil

Specifically, future climate projections predict a substantial increase in air temperature and a decrease in annual rainfall due to a higher frequency of consecutive dry days (Marengo et al. 2009). The combined effects of higher temperatures and lower rainfall in this region will lead to an 'aridification', causing an expansion of semi-deserts in the driest areas (Salazar et al. 2007; Marengo and Bernasconi 2015). However, how species of this region will respond to these climate changes and which species are sensitive or resistant to drier and hotter climatic conditions is still unknown.

The SDTF are mostly deciduous ecosystems with global relevance, because they occupy a large area in the tropics and play an important role on Earth's carbon cycle (Alström et al. 2015). Additionally, they are much more threatened by deforestation than rainforests (Olivares and Medina 1992). Global models of biogeography, vegetation, and carbon balance still consider deciduous and evergreen species as the two main functional categories for this vegetation (*see* Bonan et al. 2003; Reich et al. 2007). This has major implications for modeling ecosystem carbon and water balance because deciduous species have much shorter windows of opportunity for carbon gain and water loss than evergreen species. Deciduous species in some STDF exhibit higher gas exchange capacity, assimilation rate, and water use compared to evergreen species (Goldstein et al. 1989; Mediavilla and Escudero 2003; Miyazawa and Kikuzawa 2005; Fu et al. 2012; Worbes et al. 2013), but this pattern has not been consistently observed in all tropical deciduous ecosystems (Damesin et al. 1998; Bucci et al. 2005; Hasselquist et al. 2010). Additionally, the simple categorization in evergreen versus deciduous habit gives little insight about the whole range of existing ecological strategies in seasonally dry tropical ecosystems (Holbrook et al. 1995). Therefore, a more comprehensive dataset linking leaf phenology to ecophysiology and hydraulic strategies for these systems is needed to improve classification of plant functional types (PFTs) in land surface models (Bonan et al. 2003; Atkin et al. 2015).

The functional differences between deciduous and evergreen species are usually related to the balance between the costs and benefits of leaf construction (Chabot and Hicks 1982; Sobrado 1991; Wright et al. 2004) and growth strategies (Tomlinson et al. 2014). However, phenological groups might also be associated with contrasting stem traits such as wood density and capacitance, and these traits can be good predictors of the hydraulic functioning of plants in seasonal climates (Borchert 1994; Sobrado 1997; Brodribb et al. 2002, 2003; Brodribb and Holbrook 2005; Choat et al. 2006; Worbes et al. 2013; Gleason et al. 2015). For example, deciduous species exhibit phenological variations associated with xylem water potential (Ψ_{xylem}) and wood density (ρ_{wood}). Species with low ρ_{wood} show leaf sprouting and reproductive phases in the dry period, whereas leaf shedding and resprouting in species with high ρ_{wood} is

usually dependent on soil water availability (Borchert 1994; Borchert and Rivera 2001; Lima and Rodal 2010; Lima et al. 2012; Oliveira et al. 2015). Furthermore, the leaf life span (LL) can be associated with other two important mechanisms: leaf fall functioning like a "hydraulic fuse" avoiding damage in hydraulic vulnerable xylem during drought (Wolfe et al. 2016; Lima et al. 2018), and deep roots allowing access to deeper water sources, which extend the duration of foliage in the tree canopy during the dry season (Hasselquist et al. 2010).

In a study carried out in a Brazilian tropical savanna experiencing a 5-month dry season, woody species with different phenological behaviors (deciduous, brevideciduous, and evergreen) showed convergence in their hydraulic strategies (Bucci et al. 2005). However, evergreen species occurring in Mediterranean climate sites (*i.e.,* dry summers and wet winters) showed a more conservative hydraulic strategy in terms of water use (isohydric), as they had low maximum stomatal conductance (g_s), high stomatal sensitivity to atmospheric drought, and high predawn leaf (Ψ_{leaf}) even during the dry season (Mediavilla and Escudero 2003). The deciduous species occurring in the same region were less conservative in water use (anisohydric) and showed high maximum g_s and low stomatal sensitivity to atmospheric drought (Mediavilla and Escudero 2003). Presumably, differences in stomatal regulation strategies between deciduous and evergreen species can influence the loss in hydraulic conductance during drought, given that deciduous plants tend to have higher xylem water potential at 50% loss of hydraulic conductivity (P_{50}) than evergreen species (Fu et al. 2012; Kröber et al. 2015; Lima et al. 2018).

Empirical data point to the existence of subgroups of deciduous species (*see* Lima and Rodal 2010; Lima et al. 2012; Oliveira et al. 2015), and suggest the occurrence of different patterns in the annual variation of Ψ_{wood}, and distinct drought strategies. However, these studies used commonly measured soft traits to evaluate functional differences between deciduous and evergreen species (Felsenstein 1985; Fu et al. 2012). More detailed physiological measurements and the evaluation of the effects of phylogeny with phylogenetic independent contrasts (PICs), can provide novel mechanistic insights about functional independence of groups, correlated evolution between traits, and whether the possible trait differences observed between deciduous and evergreen species are the result of evolutionary divergences (Felsenstein 1985; Webb et al. 2008).

In this study, our aim was to investigate and contrast the diversity of hydraulic strategies in DC and EV species from SDTF of the Brazilian semi-arid region. We hypothesize that (1) Leaf hydraulic strategies differ between DC and EV species and result from evolutionary divergences; and (2) DC species compensate for their short LL by being less conservative in water use; in contrast, EV should exhibit

highly conservative water use behavior which reduces negative effects of desiccation throughout the dry period. Therefore, we expect that (1) DC species will show high variation in their seasonal water potential (*see* Borchert 1994; Lima and Rodal 2010; Oliveira et al. 2015), reducing the drop in Ψ_{xylem} when they lose the leaves (*see* Wolfe et al. 2016) and stomatal behavior is less sensitive to drought and will exhibit lower regulation (anisohydric behavior); (2) EV species will show lower variations in seasonal xylem water potential (Ψ_{xylem}) and higher stomatal regulation (isohydric behavior), being more sensitive to drought; (3) DC species will be more sensitive to drought than EV, decreasing crown cover in response to decreased water availability in the dry season; (4) EV species will be more conservative in the use of water, with less daily variation in gas exchange, leaf water potential and efficiency in water use compared to DC species; and (5) leaf and stem functional traits will determine distinct functional groups and will explain the variation in LL between DC and EV species from seasonally dry tropical forest.

We studied 22 woody species commonly found in the Brazilian semi-arid region within the Caatinga domain. Our study provides evidence that species with different leaf phenologies have similar hydraulic strategies and sensitivities to drought. In addition, we demonstrate that leaf and stem traits are phylogenetically independent, and that LL is correlated with hydraulic traits such as the maximum transpiration rate per unit of water transport capacity (Λ) and stomatal behaviour.

Material and methods

Study area

This study was carried out in seasonally dry tropical forests (SDTF), which occur in northeastern Brazil, from sea level up to 500 m (Pennington et al. 2000, 2009; Moro et al. 2014, 2016; Silva et al. 2017). This vegetation is locally known as *caatinga* (Sampaio 1995). The fragment selected (protected for approximately 40 years, with negligible human activity) is located in the Curu Valley Experimental Farm (FEVC, 3°47′S, 39°16′W), 12 km to the west of the municipality of Pentecoste, state of Ceará, Brazil. Soils in this region are shallow with low water storage capacity (Sampaio 1995). Our study area is characterized as SDTF, with plant species with different phenological patterns (according to Borchert 1994; Eamus 1999). The deciduous trees are sparse and deciduous shrubs are dominant, whereas evergreen species are less abundant. Arboreal species ranged from 4 to 15 m in height, whereas shrub species ranged from 2 to 6 m (Table 1).

Extreme droughts, of variable intensity and duration, are common in the Brazilian semi-arid region (Sampaio 1995; Marengo et al. 2013). The temperature range varies little between seasons (averages of 23 ºC in the rainy season and 27 ºC in the dry season). However, the high annual solar radiation of 2800 h and potential evapotranspiration of 2000 mm year^{-1} lead to water scarcity (Araújo et al. 2004). The regional climate is classified as BSh—semi-arid, dry, with summer rains and a dry winter in the Köppen–Geiger system (Peel et al. 2007). The climatic water balance estimated with data from the past 16 years (FEVC meteorological station 2000–2016) shows a marked difference between the rainy (water replacement) and dry seasons (water loss and deficit; Fig. 1). The average annual rainfall is 708.8 mm, with the rains concentrated in January to April (rainy season), followed by a long dry season (May to December). According to Thornthwaite (1948), the aridity index (*Ia*) and annual potential evapotranspiration (PET) are 30.2 and 2342.8 mm, respectively (Fig. 1). The average annual temperature is 29 ºC (max. 34.8 ºC and min. 22.8 ºC) with relative humidity around 60%. The average annual rainfall in the 3 years preceding this study was 519.1 mm (~73% lower than the average).

Sampling design and model species

We set up a grid of 50 continuous plots 10 × 10 m in an area of half-hectare to sample the dominant species in the community. In total, we identified 30 woody species of shrubs and trees. However, leaf traits and gas exchange were measured in 22 species because these had more than five individuals in the area (Table 1; supporting information). The sampled species represent approximately 85% of all individuals in the area. Leaf phenology, growth form (tree, shrub, or climbing shrub), average height, and the total number of individuals per species (N) in the study area are presented in Table 1.

Soil water content and vapor pressure deficit (VPD)

To determine soil water content (SWC), we collected monthly 50 soil samples in 25 10 × 10-m plots 20 m apart from one another and evenly distributed along a half-hectare area. Data collection was carried out from December 2012 to November 2013 from 07:00 to 10:00 at two depths (0–10 cm and 11–20 cm). We determined SWC (%) using the standard gravimetric method given by the difference between fresh and dry weight, which was obtained after the samples were oven dried at 105 ºC. Data from relative air humidity and temperature sensors (Vaisala, model HMP35C) were used to calculate monthly vapor pressure deficit (VPD), according to the formula: $VPD = es - ea$, where *es* is the saturation vapor pressure of air and *ea* is

Table 1 Leaf phenology, growth form, wood density, plant height, and number of individuals of woody plants in a half-hectare plot in Pentecoste, Ceará, northeastern Brazil

Family/species	Leaf phenology	Growth form	Wood density (g cm^3)	Plant height (m)	Number of individuals (5.000 m^2)
Apocynaceae					
Aspidosperma subincanum Mart	Deciduous	Tree	0.65	4.1±0.2	19
Bixaceae					
Cochlospermum vitifolium (Willd.) (L.) Spreng	Deciduous	Tree	0.20	8.1±0.8	23
Boraginaceae					
Cordia oncocalyx Allemão	Deciduous	Tree	0.55	7.9±2.5	106
Cordia trichotoma (Vell.) Arráb. exSteud	Deciduous	Tree	0.55	6.2±0.6	19
Burseraceae					
Commiphora leptophloeos (Mart.) J.B. Gillett	Deciduous	Tree	0.30	9.6±1.6	9
Capparaceae					
Cynophalla flexuosa (L.) J. Presl	Evergreen	Shrub	0.56	2.3±0.9	6
Combretaceae					
Combretum leprosum Mart	Deciduous	Climbing shrub	0.55	6.6±0.3	113
Euphorbiaceae					
Croton blanchetianus Baill	Deciduous	Tree	0.62	11.9±0.6	57
Manihot carthaginensis (Müll. Arg.) Allemão	Deciduous	Shrub	0.34	5.4±0.3	51
Sebastiania macrocarpa Müll. Arg	Deciduous	Tree	0.62	5.3±0.1	811
Fabaceae					
Amburana cearensis (Allemão) A.C. Sm	Deciduous	Tree	0.46	12.8±3.0	11
Anadenanthera colubrina (Griseb.) Altschul	Deciduous	Tree	0.61	7.0±1.5	6
Bauhinia cheilantha (Bong.) D. Dietr	Deciduous	Tree	0.67	8.0±0.5	122
Libidibia ferrea (Mar. ex Tul.) L.P. Queiroz	Evergreen	Tree	0.65	8.3±1.5	11
Mimosa caesalpiniifolia Benth	Deciduous	Tree	0.65	15.2±1.7	50
Piptadenia stipulacea (Benth.) Ducke	Deciduous	Tree	0.57	8.4±0.5	92
Piptadenia viridiflora (Kunth) Benth	Evergreen	Tree	0.59	7.4±0.7	11
Poincianella bracteosa (Tul.) L.P. Queiroz	Deciduous	Tree	0.65	6.8±1.1	98
Lythraceae					
Lafoensia pacari St. Hil	Deciduous	Tree	0.62	7.9±0.4	68
Malvaceae					
Helicteres heptandra L.B. Sm	Deciduous	Shrub	0.57	2.2±0.5	10
Olacaceae					
Ximenia americana L	Evergreen	Tree	0.58	8.5±0.8	25
Rhamnaceae					
Zizyphus joazeiro Mart	Evergreen	Tree	0.55	12.4±1.2	6

Patterns of leaf phenology: deciduous or evergreen. Growth form: tree, shrub, or climbing shrub. Wood density in g cm^3 (average of 25 samples per species). Plant height in m (average±standard error). Total number of individuals per species in half a hectare of the Curu Valley Experimental Farm, Pentecoste, Ceará, Brazil

water vapor pressure. We used the averages of daily values of relative humidity and average maximum temperature in the interval of maximum radiation 9 am to 3 pm. We used these daily averages to estimate monthly VPD. All climate data were obtained from the FEVC meteorological station.

Field measurement of leaf traits

We measured 17 leaf traits to characterize leaf functional differences of deciduous and evergreen species, following the protocol proposed by Pérez-Harguindeguy et al.
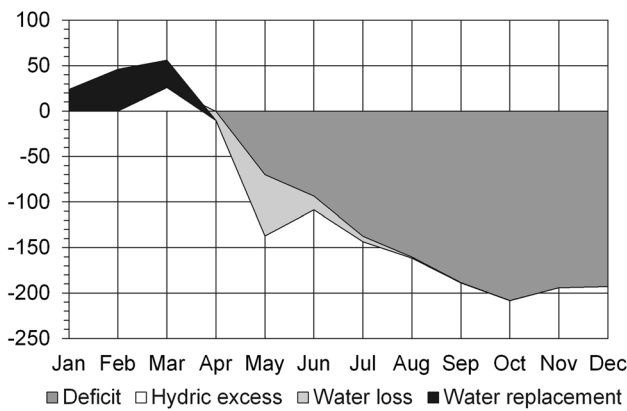
Fig. 1 Climate water balance for the Curu Valley Experimental Farm, Pentecoste, Ceará, northeastern Brazil. We present data for the past 16 years (meteorological station 2000–2016; annual rainfall: 708.8 mm, annual evapotranspiration: 2342.8 mm, annual water deficit: 1634 mm and index aridity:30.2). *Thornthwaite Water Balance (BHídrico GD 4.0 – 2004)*

(2013). All leaf and stem traits measured are summarized in Table 2. Due to the logistical difficulties of tagging and monitoring branches with leaves in adult trees, we assumed leaf life span (LL; in days) to be the average number of days from the beginning of leaf sprouting to leaf fall, which we monitored in ten individuals per species at 15-day intervals. We also estimated the monthly crown cover dynamics by determining the canopy coverage from direct monthly observations of the crown leaf cover using the index of intensity of phenology activity proposed by Fournier (1974). The index consisted in estimating the leaf coverage for all species attributing a continuous percentage value of crown cover range 0–100%. To measure the other leaf traits, we used ten expanded leaves from five individuals per species (50 leaves per species). All leaves were sun-exposed and damage free. In April 2013, we collected leaves from 08:00 to 10:00, rehydrated them for 8 h before measuring leaf area (LA; cm^2), petiole length (PL; cm), leaf dry mass per area (LMA; dry mass/leaf area; $mg^{-1} mm^2$), leaf thickness (LTh; mm), leaf density (LD; dry mass /(leaf area x leaf thickness; $g\ cm^{-3}$), leaf dry matter content (LDMC; dry mass /water-saturated fresh mass; $mg\ g^{-1}$), leaf saturated water content (SWC_{leaf}; water-saturated fresh mass–dry mass / dry mass; $g\ g^{-1}$), leaf succulence (LS; water-saturated fresh mass–dry mass/leaf area; g/m^2), chlorophyll per unit leaf area (Chl_{area}; chlorophyll content/leaf area; $\mu mol\ cm^{-2}$), and chlorophyll per unit mass (Chl_{mass}; chlorophyll content/mass; $\mu mol\ g^{-1}$).

Table 2 Comparison of 17 leaf traits among 17 deciduous and five evergreen species and phylogenetically independent contrasts (values represent average ± standard error)

Leaf trait	Abbreviation	Unit	Deciduous	Evergreen	F	P	PIC obs	PIC rand	P
Leaf life span	LL	Days	159.0 ± 10.7	326.8 ± 17.4	29.01	**0.000**	8.40E+01	7.79E+01	0.669
Leaf area	LA	cm^2	85.0 ± 16.6	33.4 ± 13.0	4.50	**0.046**	5.00E+01	4.86E+01	0.595
Petiole length	PL	cm	27.8 ± 9.5	10.7 ± 2.6	1.06	0.313	1.30E+01	1.41E+01	0.450
Leaf dry mass per area	LMA	$mg^{-1} mm^2$	0.03 ± 0.0	0.09 ± 0.0	30.65	**0.000**	8.87E−06	8.65E−06	0.597
Leaf thickness	LTh	mm	0.21 ± 0.02	0.21 ± 0.05	0.06	0.797	7.16E−05	9.85E−05	0.105
Leaf density	LD	$g\ cm^{-3}$	0.23 ± 0.03	0.53 ± 0.09	10.45	**0.004**	4.95E−04	4.18E−04	0.781
Leaf dry matter content	LDMC	$mg\ g^{-1}$	315.2 ± 19.7	463.3 ± 28.9	12.33	**0.002**	8.38E+01	1.11E+02	0.130
Leaf saturated water content	SWC_{leaf}	$g\ g^{-1}$	2.48 ± 0.2	1.22 ± 0.15	13.85	**0.001**	5.85E−03	9.64E−03	**0.022**
Leaf succulence	LS	g/m^2	90.8 ± 32.4	114.9 ± 24.3	1.10	0.306	1.12E+01	1.66E+01	0.050
Chlorophyll per unit leaf area	Chl_{area}	$\mu mol\ cm^{-2}$	1.8 ± 1.1	5.03 ± 1.1	29.22	**0.000**	9.82E−02	5.68E−02	0.951
Chlorophyll per unit mass	Chl_{mass}	$mgmol\ g^{-1}$	2.24 ± 0.38	4.88 ± 0.73	7.88	**0.010**	5.12E+02	4.01E+02	0.885
Leaf maximum area-based photosynthesis rate	A_{max}	$\mu mol\ CO_2\ m^{-2}\ s^{-1}$	8.29 ± 0.6	7.38 ± 0.9	0.41	0.527	8.61E−02	8.22E−02	0.632
Leaf maximum mass-based photosynthesis rate	A_m	$nmol\ CO_2\ g^{-1}\ s^{-1}$	232.2 ± 25.6	80.8 ± 10.9	21.48	**0.000**	1.86E+02	1.45E+02	0.881
Maximum stomatal conductance	gs_{max}	$mol\ H_2O\ m^{-2}\ s^{-1}$	0.37 ± 0.02	0.31 ± 0.03	1.56	0.225	2.00E−04	1.43E−04	0.931
Water-use intrinsic efficiency	WUE	$\mu mol\ CO_2\ mol^{-1}\ H_2O$	23.0 ± 1.7	24.8 ± 3.8	0.21	0.645	7.84E−01	6.51E−01	0.837
Nitrogen per unit mass	N_{mass}	$mg\ g^{-1}(\%)$	2.48 ± 0.1	2.19 ± 0.1	1.02	0.322	2.73E−03	2.58E−03	0.643
Phosphorus per unit mass	P_{mass}	$mg\ g^{-1}(\%)$	0.20 ± 0.02	0.17 ± 0.02	0.24	0.629	5.30E−05	7.43E−05	0.175

Average values of two phenological groups compared with a one-way ANOVA for independent samples and *P*-values < 0.05 are shown in boldface. The phylogenetically independent contrasts PIC obs.—observed and PIC rand.—randomized were calculated for each trait and *P* value < 0.025 are shown in boldface

We estimated chlorophyll content using a SPAD chlorophyll meter (Minolta SPAD 502 Chlorophyll Meter, Spectrum Technologies Inc., Plainfield, IL, USA), and, then, we used the average value to calculate the polynomial model for tropical trees (chlorophyll content $= 0.664 \times SPAD + 0.012 \times SPAD^2$; Coste et al. 2010). We measured the physiological leaf traits one time during the rainy season. To measure the maximum photosynthesis rate per unit area (A_{max}; µmol m^{-2} s^{-1}), the maximum photosynthesis rate per unit mass (A_m; $A_m = A_{max}$/LMA; nmol g^{-1} s^{-1}), and the maximum stomatal conductance (gs_{max}; mol m^{-2} s^{-1}), we used a handheld infrared gas analyzer (Model LI-6400XT; LI-COR Inc., Lincoln, NE, USA). For measurements of gas exchange, we kept the leaves in the chamber of the handheld meter for approximately 120 s; the CO_2 concentration was fixed at 400 ppm, the flow rate 400 µmol s^{-1}, and the photosynthetically active radiation inside the chamber was 1800 µmol (LI-6400XT LED light source). We took the measurements from 08:00 to 10:00 on clear days. The relative humidity at natural conditions varied from 50 to 70% and the temperature from 25 to 32 ºC. We also calculated the intrinsic water use efficiency (WUE; A_{max}/gs_{max}; µmol CO_2 mol^{-1} H_2O). Using the same leaves from which we measured all traits, we determined the nitrogen content per unit mass (N_{mass}; % dry mass) and the phosphorus content per unit mass (P_{mass}; % dry mass) per individual. We determined leaf total nitrogen content using the micro-Kjeldahl method (Bremner 1965). To determine leaf total phosphorus content, after distillation, we used a mixture of nitric, sulfuric, and perchloric acids, at the proportion 10:1:2. The total phosphorus in the extract was determined by colorimetry, at 410 nm, using ammonia vanadomolybdate (Allen et al. 1974).

Field measurements of stem water potential, wood density, and gas exchange

To investigate the water relations of each species in the rainy and dry seasons, we measured each month the predawn xylem water potential ($\Psi_{xylemPD}$; MPa) using a Scholander pressure chamber with a maximum capacity of 10 MPa (Model P3005F01, Soil Moisture Corp., Santa Barbara, California, USA). We carried out $\Psi_{xylemPD}$ measurements on three terminal branches of three individuals per species. We decided to use terminal branches, because during the dry season deciduous species lose their leaves completely. Measuring water potential in leafless terminal branches with a pressure chamber can accurately represent Ψ_{xylem} (Wolfe and Kursar 2015). We opted to measure predawn water potential (Ψ_{PD}) on branches that were not isolated in black plastic bags after we discarded the hypothesis of nocturnal transpiration by testing for differences in Ψ_{leaf} between bagged and unbagged branches.

We assumed that the soil water potential at the root level equals the $\Psi_{xylemPD}$ on terminal branches (Brodribb et al. 2002), except for species with water storage capacity (stem succulents) that maintained high water potential regardless of the soil water potential (*C. leptophloeos, A. cearensis, C. vitifolium* and *M. carthaginensis; see* Lima and Rodal 2010; Oliveira et al. 2015). We measured the $\Psi_{xylemPD}$ from December 2012 to November 2013, from 0:00 to 4:00 on the 15th day of each month. We obtained the minimum seasonal water potential ($\Psi_{xylemPD\,minimum}$; MPa) by considering the minimum value of water potential observed during the year. To investigate the relationship between the $\Psi_{xylemPD}$ and wood density (ρ_{wood}; g cm^3), we measured ρ_{wood} in five branch samples (diameter ≥ 3 cm) of five individuals per species. Each sample was peeled, saturated in distilled water for 120 h to determine its volume and then oven dried for 72 h at 105 ºC (Pérez-Harguindeguy et al. 2013). We determined the ρ_{wood} by calculating the ratio between the dry mass and the saturated volume.

To assess the stomatal behavior, photosynthesis, and leaf water status of the species throughout the day, we measured the daily variation in stomatal conductance (g_s), photosynthesis rate (A), the leaf water potential (Ψ_{leaf}) and WUE in five individuals per species. We carried out the measurements of gas exchange in rainy season (April 2014) and Ψ_{leaf} in the rainy and beginning dry season (April 2014, May 2015 and June 2016). All measurements were made on clear days from 4:00 to 18:00 at 2 h intervals, using five leaves per individual. We used Ψ_{PD} and the water potential at midday (Ψ_{MD}) to assess the stomatal regulation strategies in response to drought (Martínez-Vilalta et al. 2014). In addition, we tested for differences among species in terms of the water potential responsible for 50% of stomatal closure (Ψ_{SC}; MPa; Brodribb et al. 2003). To calculate the Ψ_{SC}, we used the measurements of Ψ_{leaf} and g_s only in times of the day when light was saturating (10:00 and 12:00 pm). All measurements were taken from damage-free leaves that were exposed to full sun. We divided the 22 species in pairs and measured them for 11 consecutive days, to minimize the effects of climate variations.

We kept the leaves in the chamber of the infrared analyzer for 120 s; the CO_2 concentration was fixed at 400 ppm, the flow rate at 400 µmol s^{-1}, and the humidity in the chamber was similar to that of the ambient conditions. We calculated the photosynthetically active radiation (PAR) inside the chamber (LI-6400XT LED light source) as the averages per time (4:00–0 µmol; 6:00–300 µmol; 8:00–1200 µmol; 10:00–1800 µmol; 12:00–2000 µmol; 14:00–1200 µmol; 16:00–400 µmol; 18:00–0 µmol) obtained in clear days with the quantum sensors LI-191 connected to a data logger LI-1400 (LI-COR Inc., Lincoln, NE, USA). Immediately after the measurement of g_s, we placed the leaves in a Scholander pressure chamber to measure Ψ_{leaf}.

Statistical analysis

We tested for differences in leaf functional traits between DC and EV species with a multivariate analysis of variance (one-way MANOVA) for independent samples using R (R Development Core Team 2015). The data were tested for normality (Shapiro–Wilk test), and, if necessary, log-transformed (base 10) before undergoing parametric tests. To identify the specific dependent variables that contributed to the significant global effect, we used the univariate one-way ANOVA. Additionally, we used the Bonferroni correction to adjust the alpha significance ($\alpha < 0.05$), each individual test because the groups have different sample sizes.

To evaluate whether the observed differences in leaf and stem traits between DC and EV species are the result of evolutionary divergences, we calculated phylogenetically independent contrasts (PIC's) as described in Webb et al. (2008). We constructed a working phylogenetic tree with the 22 species analyzed from the supertree R20160415 using the software 'Phylocom' version 4.2 (Webb et al. 2008). We compared the PIC's values observed with the PIC's randomly swapping each trait values across the tree, with 999 randomizations. We considered there was a phylogenetic signal when observed PIC's were statistically different from randomized mean PIC's (P value < 0.025; Münkemüller et al. 2012). We used the package "Picante" in R (Kembel et al. 2010) for this analysis. For each trait, we measure the signal intensity using the Blomberg's K coefficient (Blomberg et al. 2003).

To assess the stomatal regulation strategies of the species in response to the loss of conductivity during drought we used the approach proposed by Martínez-Vilalta et al. (2014). We plotted a linear regression with Ψ_{PD} as independent variable (x) and Ψ_{MD} as dependent variable (y) and used the slope value (σ) to categorize the species according to stomatal behaviour (isohydry to anisohydry) and used the intercept value (Λ) to estimate the maximum transpiration rate per unit of water transport capacity (Martínez-Vilalta et al. 2014). We tested for differences in σ and Λ between the groups with a t test for independent samples.

To investigate which groups are more sensitive to drought, we used simple and multiple regression models to test which environmental variables, VPD (kPa) and SWC (%), significantly affect species crown cover (%). We used a regression analysis to test the relationship between wood density (ρ_{wood}) with minimum predawn ($\Psi_{xylemPD\ minimum}$) and LL with hydraulic strategies descriptors (Ψ_{SC}, σ, and Λ). We also used a one-way ANOVA followed by a Bonferroni post hoc test ($\alpha < 0.05$) to compare phenological groups in relation to daily variation in g_s, A, Ψ_{leaf}, and WUE. All these analyzes were carried out in R (R Development Core Team 2015).

Finally, to examine combined patterns of functional traits and species ordination in relation to phenological behavior and hydraulic strategies, we performed a principal component analysis (PCA) using the software PC-ORD 6 (Multivariate Analysis of Ecological Data, Oregon, U.S.A). In this analysis, we used the minimum number of functional traits after observing a high correlation between many traits. We used multi-response permutation procedures (MRPP) based on the Euclidian distance to compare functional similarity within the groups formed after the PCA. The MRPP does not use assumptions such as multivariate normality and homogeneity of variances. This analysis provides an 'A-value' that varies between 0–1 and can be used as a proxy for within-group homogeneity (McCune and Mefford 2011). We considered the functional groups consistent, if the 'A-value' was larger than 0.3 (McCune and Grace 2002).

Results

Differences in leaf traits between evergreen and deciduous species

We observed marked differences between phenological groups in traits related to carbon assimilation and investment in leaf construction (one-way MANOVA $F = 122.3$, $P < 0.0001$). Leaf life span (LL) differed between EV (326.8 days) and DC species (159.0 days; Table 2). Leaf area (LA), SWC_{leaf}, and A_m were significantly higher for DC than EV species (Table 2). Nevertheless, LMA, LD, LDMC, Chl_{area}, and Chl_{mass} were higher in EV than DC species (Table 2). There were no differences in PL, LTh, LS, A_{max}, gs_{max}, WUE, N_{mass}, and P_{mass} between DC and EV species (Table 2). All leaf traits demonstrated weak phylogenetic signal intensity indicated by Blomberg K coefficient values < 1, except SWC_{leaf} that presented significant signal and $K = 0.76$ (supplementary data Table S1). The signal was not significant for these traits when compared with randomized PIC, indicating phylogenetical independency between groups (Table 2).

Seasonal maintenance of water status

All species reached their maximum $\Psi_{xylemPD}$ after the month with the highest rainfall, then gradually decreased until reaching the $\Psi_{xylemPD\ minimum}$ in the end of the dry season (Fig. 2). The $\Psi_{xylemPD}$ varied between -0.1 and -8.3 MPa in DC species, and between -0.6 and -7.0 MPa in EV species across seasons (Fig. 2). Only one evergreen species (*X. americana*) showed high variation in $\Psi_{xylemPD}$ between seasons and $\Psi_{xylemPD\ minimum}$ of -7.0 MPa, similar behavior to most deciduous species (Fig. 2a). Only four DC species (*A. subicanum*, *C. leprosum*, *P. stipulacea* and *P. bracteosa*)
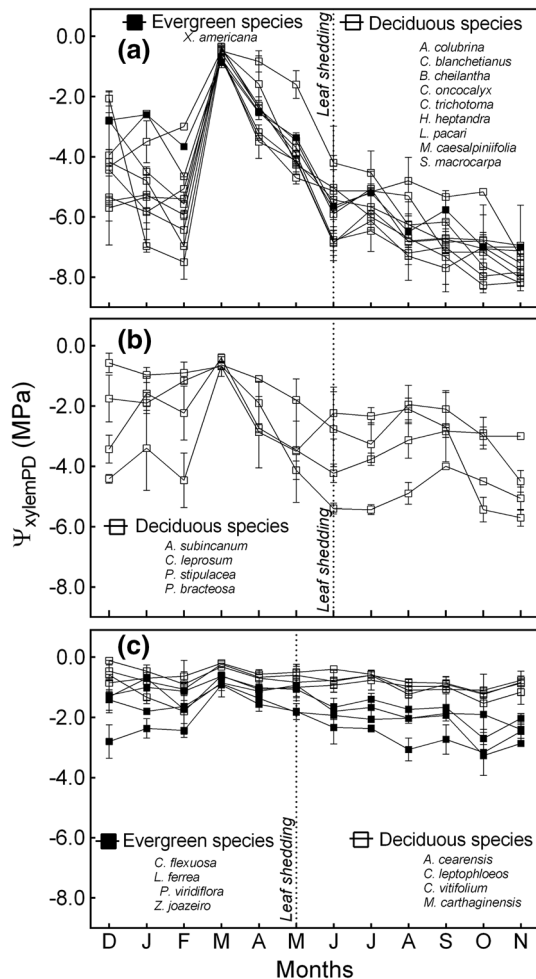
Fig. 2 Annual patterns in predawn stem water potential (Ψ_{PD}) in 17 deciduous and 5 evergreen species. In **a** Deciduous and only evergreen species with high variation; **b** only deciduous species reduce the variation after leaf shedding; and **c** deciduous and evergreen species with low variation. *Open square—deciduous species; black square—evergreen species. Dot line—average of leaf shedding in three individuals for species*

Fig. 3 Relation between minimum seasonal xylem water potential ($\Psi_{xylemPD}$) and wood density (ρ_{wood}) for 17 deciduous and 5 evergreen species. Symbols represent ρ_{wood}—average of five individuals and $\Psi_{xylemPD}$—average of three individuals for species. *Open square— deciduous species; black square—evergreen species*

on the rainfall regime to rehydrate or lost the leaves to avoid greater drops in $\Psi_{xylemPD}$, whereas the other evergreen with high ρ_{wood} and deciduous species with low ρ_{wood} either had deep roots and/or relied on stored water to maintain a stable $\Psi_{xylemPD}$.

We found a strong negative relation between ρ_{wood} and $\Psi_{xylemPD\ minimum}$ in all species (polynomial model, $r^2 = 0.73$, $P < 0.001$; Fig. 3). Deciduous species with low regulation of water status between seasons showed high ρ_{wood} and more negative $\Psi_{xylemPD\ minimum}$ (Fig. 3). In contrast, DC species with low ρ_{wood} showed the least negative $\Psi_{xylemPD\ minimum}$ among all species studied (Fig. 3). All EV species showed high ρ_{wood} related to less negative $\Psi_{xylemPD\ minimum}$, but *X. americana* showed a $\Psi_{xylemPD\ minimum}$ similar to those of DC species with high ρ_{wood} (Fig. 3).

Stomatal regulation strategies and gas exchange

Unlike our predictions, we observed that DC and EV species showed similar behavior in terms of stomatal control and plant conductivity loss in response to drought (Fig. 4a–v). The average values of slope (σ) of linear regressions between Ψ_{PD} and Ψ_{MD} for all species was similar for two groups, deciduous (0.77 ± 0.07 MPa MPa^{-1}) and evergreen species (0.65 ± 0.05 MPa MPa^{-1}; $t = -0.84$ $P > 0.05$; Fig. 4a–v). Most species, regardless of their phenological group, showed partially isohydric behavior, indicating more control in stomatal aperture to water loss (Fig. 4a–v). In DC species, only *C. blanchetianus* exhibited extreme anisohydric behavior (Fig. 4j).

Deciduous species showed lower transpiration rate per unit of hydraulic conductivity (Λ) than evergreen species (DC—. 0.35 ± 0.12; EV $= -2.41 \pm 0.16$; $t = -4.19$ $P < 0.0001$; Fig. 4a–v). The similarities in hydraulic strategies between DC and EV species are also confirmed by daily variation in gas exchange and Ψ_{leaf} (Fig. 5a–d). During the day, DC species exhibited higher g_s than EV species

reduced the drop in $\Psi_{xylemPD}$ after leaf shedding, while other four species (*M. carthaginensis*, *C. vitifolium*, *A. cearensis*, and *C. leptophloeos*) exhibited low variation in $\Psi_{xylemPD}$ between the dry and rainy seasons (Fig. 2b, c).

We found three patterns of seasonal maintenance in water status related with ρ_{wood} and leaf shedding that were independent of the two phenological categories: (1) species with high ρ_{wood} that depended on soil water availability to increase their water status, but could not maintain their status after leaf shedding in the end of rainy season; (2) species that shed leaves early in the dry season showed less variation in their water status; and (3) species with a regular maintenance of their water status regardless of the rainfall regime and duration of leaves (Fig. 2a–c). Deciduous species with high ρ_{wood} and the evergreen species *X. americana* depended
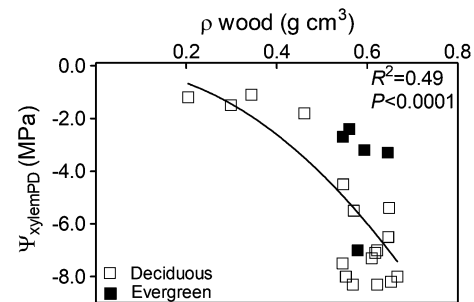
($F = 10.12$ $P < 0.05$), but in the hours of higher photosynthetic activity (10 am to 2 pm), the groups showed no differences ($t = 1.05$; 2.34; 2.67 $P > 0.05$; Fig. 5a). In relation to photosynthetic rates (A), the groups were similar ($F = 1.97$ $P > 0.05$; Fig. 5b). Although DC exhibited higher g_s than EV species, the Ψ_{leaf} was less negative in DC species in the morning (8 and 10 am; $t = 4.32$; 4.83 $P < 0.001$) but in the rest of the day, it was not different relative to EV species ($F = 1.63$ $P > 0.05$; Fig. 5c). The phenological groups had similar WUE at all times ($F = 2.02$ $P > 0.05$; Fig. 5d).

Effects of VPD and SWC on crown-cover dynamics

The VPD and SWC were strongly correlated with seasonal dynamics in crown cover (%) of DC and EV species (Fig. 6a, b). We observed different critical points in VPD affecting crown cover (%) in DC and EV species (Fig. 6b). Deciduous species had synchrony between maximum crown cover (%) and VPD values below 1.0 kPa (Fig. 6b). The crown cover (%) in EV species was not affected by VPD, even at the peak of the dry season, when the monthly VPD average was above 2.0 kPa (Fig. 6b; Table 3).

In DC species, crown cover (%) was positively related to SWC (simple regression, $r^2 = 0.67$, $P < 0.05$) and VPD (simple regression, $r^2 = 0.69$, $P < 0.01$; Table 3). By analyzing the variation in SWC and VPD in relation to crown cover (%) in DC species (multiple regression, $r^2 = 0.86$, $P < 0.001$; Table 3), we observed high sensitivity to the pooled effects of the atmospheric and edaphic drought. In the case of EV species, we observed a significant linear correlation only with SWC (simple regression, $r^2 = 0.58$; $P < 0.05$) and no correlation with VPD (simple regression, $r^2 = 0.25$; $P = 0.77$; Table 3). Crown cover (%) in EV species showed sensitivity only to edaphic drought. Even when performing a pooled analysis of SWC and VPD, there were no significant differences when we compared these multiple models with the simple model only with SWC (multiple regression, $r^2 = 0.58$; $P < 0.05$; Table 3).

Interplay between leaf phenology and hydraulic traits

The variation in LL was weakly explained by the slope value (σ) that represents the isohydric and anisohydric behavior of the species (Fig. 7a). In contrast, the transpiration rate per unit of hydraulic conductivity (Λ) was the hydraulic trait more strongly correlated with LL (Fig. 7b). The negative linear relationship between LL and Λ indicates that species with high LL are less vulnerable to loss in hydraulic conductivity than species that lose their leaves (Fig. 7b). The LL was also negatively correlated with the water potential responsible for 50% of stomatal closure (Ψ_{SC}; Fig. 7c). This relationship indicates that species with high LL tolerate

the increase in negative pressure (low Ψ_{leaf}) before stomata closes and consequently, are hydraulically safer than early-deciduous species.

Functional leaf and stem traits predict phenology groups and hydraulic strategies

In the principal component analysis (PCA), the first principal component represented in the PC1 axis explained 48.2% of the variation in leaf and hydraulic traits (Fig. 8). As expected, leaf traits, such as LL and LMA and hydraulic traits Λ and Ψ_{SC}, reflect a contrast between leaf construction costs and low hydraulic safety. Therefore, they were grouped oppositely and strongly loaded in the principal component 1 (PC1; Fig. 8a). Although the species were found in many directions, only those two morphological traits (LL and LMA) were strong enough to separate species according to phenological types (Fig. 8b). The second principal component, PC2, explained 18.6% of the variation in trait values (Fig. 8). Only A_{max} had a strong positive effect in relation to PC2 and was not crucial to separate the species according to assimilation rate (Fig. 8b). The result of the MRPP test showed a strong consistency in the groups formed based on the ordination of leaf and hydraulic traits ($A = 0.46$; $P < 0.001$). The PC1 axis was independent of the PC2 axis indicating that the cost for leaf longevity and hydraulic safety are strongly dissociated from their assimilation of CO_2. The magnitude of eigenvalues and eigenvectors are shown in the supplementary data Table S2.

Discussion

Our findings demonstrate that deciduous and evergreen species have slight differences in hydraulic strategies but also highlight greater divergence in hydraulic behavior within deciduous species. Differences in functional leaf traits support the well-known tradeoff between maximization of carbon gain and leaf longevity. However, we demonstrate that both groups exhibit similar degrees of isohydric behavior and significant stomatal control before loss in hydraulic conductivity. Additionally, we provide evidence that leaf shedding (deciduousness) does not necessarily stabilize stem water potential during the dry season in some deciduous species.

The functional leaf traits that differ between DC and EV species are related to leaf structure. Deciduous species invest less mass per unit leaf area while evergreen species have higher leaf mass per area. These results are consistent with the studies conducted in other seasonally dry ecosystems (Sobrado 1991; Eamus 1999; Ishida et al. 2006; Powers and Tiffin 2010; Fu et al. 2012); however, we did not find differences in physiological traits (A_{max} and g_{smax}) in contrast
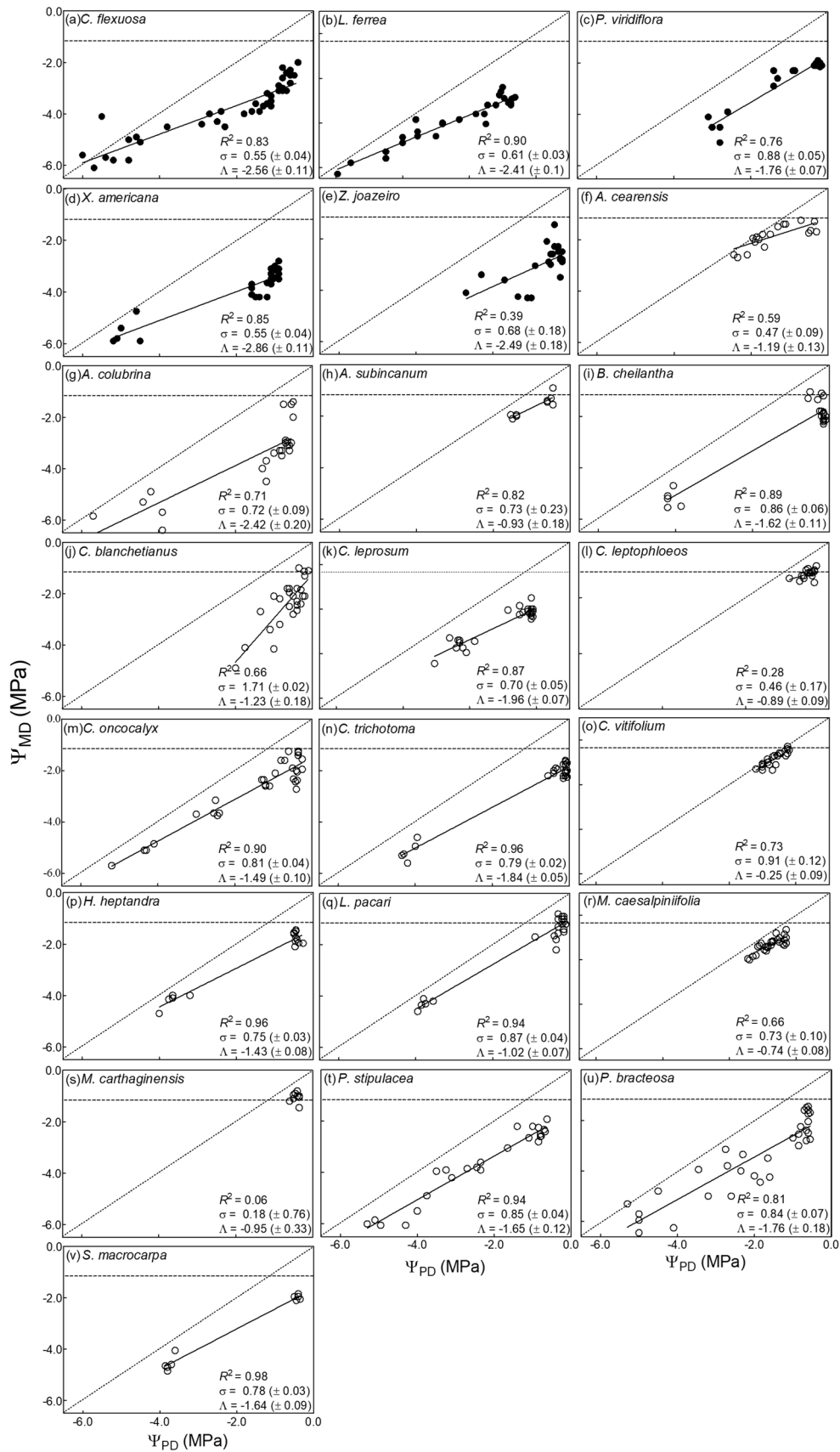
(a)*C. flexuosa*
$R^2 = 0.83$
$\sigma = 0.55\ (\pm 0.04)$
$\Lambda = -2.56\ (\pm 0.11)$

(b)*L. ferrea*
$R^2 = 0.90$
$\sigma = 0.61\ (\pm 0.03)$
$\Lambda = -2.41\ (\pm 0.1)$

(c)*P. viridiflora*
$R^2 = 0.76$
$\sigma = 0.88\ (\pm 0.05)$
$\Lambda = -1.76\ (\pm 0.07)$

(d)*X. americana*
$R^2 = 0.85$
$\sigma = 0.55\ (\pm 0.04)$
$\Lambda = -2.86\ (\pm 0.11)$

(e)*Z. joazeiro*
$R^2 = 0.39$
$\sigma = 0.68\ (\pm 0.18)$
$\Lambda = -2.49\ (\pm 0.18)$

(f)*A. cearensis*
$R^2 = 0.59$
$\sigma = 0.47\ (\pm 0.09)$
$\Lambda = -1.19\ (\pm 0.13)$

(g)*A. colubrina*
$R^2 = 0.71$
$\sigma = 0.72\ (\pm 0.09)$
$\Lambda = -2.42\ (\pm 0.20)$

(h)*A. subincanum*
$R^2 = 0.82$
$\sigma = 0.73\ (\pm 0.23)$
$\Lambda = -0.93\ (\pm 0.18)$

(i)*B. cheilantha*
$R^2 = 0.89$
$\sigma = 0.86\ (\pm 0.06)$
$\Lambda = -1.62\ (\pm 0.11)$

(j)*C. blanchetianus*
$R^2 = 0.66$
$\sigma = 1.71\ (\pm 0.02)$
$\Lambda = -1.23\ (\pm 0.18)$

(k)*C. leprosum*
$R^2 = 0.87$
$\sigma = 0.70\ (\pm 0.05)$
$\Lambda = -1.96\ (\pm 0.07)$

(l)*C. leptophloeos*
$R^2 = 0.28$
$\sigma = 0.46\ (\pm 0.17)$
$\Lambda = -0.89\ (\pm 0.09)$

(m)*C. oncocalyx*
$R^2 = 0.90$
$\sigma = 0.81\ (\pm 0.04)$
$\Lambda = -1.49\ (\pm 0.10)$

(n)*C. trichotoma*
$R^2 = 0.96$
$\sigma = 0.79\ (\pm 0.02)$
$\Lambda = -1.84\ (\pm 0.05)$

(o)*C. vitifolium*
$R^2 = 0.73$
$\sigma = 0.91\ (\pm 0.12)$
$\Lambda = -0.25\ (\pm 0.09)$

(p)*H. heptandra*
$R^2 = 0.96$
$\sigma = 0.75\ (\pm 0.03)$
$\Lambda = -1.43\ (\pm 0.08)$

(q)*L. pacari*
$R^2 = 0.94$
$\sigma = 0.87\ (\pm 0.04)$
$\Lambda = -1.02\ (\pm 0.07)$

(r)*M. caesalpiniifolia*
$R^2 = 0.66$
$\sigma = 0.73\ (\pm 0.10)$
$\Lambda = -0.74\ (\pm 0.08)$

(s)*M. carthaginensis*
$R^2 = 0.06$
$\sigma = 0.18\ (\pm 0.76)$
$\Lambda = -0.95\ (\pm 0.33)$

(t)*P. stipulacea*
$R^2 = 0.94$
$\sigma = 0.85\ (\pm 0.04)$
$\Lambda = -1.65\ (\pm 0.12)$

(u)*P. bracteosa*
$R^2 = 0.81$
$\sigma = 0.84\ (\pm 0.07)$
$\Lambda = -1.76\ (\pm 0.18)$

(v)*S. macrocarpa*
$R^2 = 0.98$
$\sigma = 0.78\ (\pm 0.03)$
$\Lambda = -1.64\ (\pm 0.09)$

Ψ_{MD} (MPa)

Ψ_{PD} (MPa)

with some studies (Mediavilla and Escudero 2003; Ishida et al. 2006; Chen et al. 2009). These results suggest that both EV and DC species diverge in leaf functional traits but may converge in other functions.

In general, the PIC's indicated that the leaf and stem traits from DC and EV species analyzed have a weak phylogenetic signal and that the phylogenetically close species tend to be functionally distinct. This result suggests a weak divergent selection in leaf and stem traits that differentiate DC from EV species, and which does not depend on phylogenetic proximity. The weak conservatism of these traits may be due to environmental filtering, which should select taxa that are functionally more similar, but phylogenetically more distant (Webb et al. 2002).

We found that DC and EV species exhibit similar degrees of isohydric behavior, which contradicts our hypothesis that only EV species had more conservative behavior in water use. The isohydric behavior means that early stomatal closure during the dry period can maintain high leaf water potential (Ψ_{leaf}) values and the plants avoid water stress at the expense of lower carbon uptake (Martínez-Vilalta

et al. 2014; Vico et al. 2014). Commonly, stomatal closure strongly depends on atmospheric water demand and soil water available (Buckley 2005) and trees from sem-iarid regions exposed to higher vapour pressure deficits (VPD) tend to experience lower daily Ψ_{leaf} regardless of leaf habit (Klein 2014). The convergence of stomatal behavior observed in DC and EV species confirms that under certain environments and conditions, leaf phenology cannot predict hydraulic traits and water use strategies in response to drought (Borchert 1994; Brodribb et al. 2002; Bucci et al. 2004; Ishida et al. 2010; Markesteijn et al. 2011).

The leaf life span in DC species responded both to atmospheric (VPD) and edaphic drought (SWC), whereas EV species responded only to edaphic drought. Two main factors are important to determine leaf fall in response to drought: (1) duration and intensity of the dry season and (2) the capacity of each species to control water loss (Borchert 1994). Commonly, leaf fall in DC species is considered as a mechanism to avoid transpiration and favor the maintenance of high tissue water potential (Levitt 1980; Reich and Borchert 1982; Borchert et al. 2002; Markesteijn and Poorter 2009). In contrast, maintenance of leaves during the entire year and sprouting of new leaves in the dry season in evergreen species are attributed to the capacity of their root systems to obtain deep water from the soil (Borchert 1994; Ackerly 2004) or to stem capacitance (Jackson et al. 1997). Strong stomatal control throughout the year can also contribute to the maintenance of a favorable water status for a longer time (Mediavilla and Escudero 2003).

The central prediction of the hydraulic fuse hypothesis is that leaf shedding minimizes hydraulic stress in the xylem (Tyree et al. 1993). We found that after leaf shedding for several deciduous speciesm, the xylem water potential (Ψ_{xylem}) continued to drop. Similar results were described by Wolfe et al. (2016) when testing the hydraulic fuse hypothesis for

Fig. 5 Behavior of stomatal conductance (g_s), photosynthesis rate (A), leaf water potential (Ψ_{leaf}) and water use efficiency (WUE) daily in 17 deciduous and 5 evergreen species. Average g_s (**a**), average A (**b**), average Ψ_{leaf} (**c**) and average WUE (**d**) in five individuals for species by daytime. *Comparison between deciduous and evergreen species for variance analysis (ANOVA and Tukey test $\alpha < 0.05$). Open square—deciduous species; black square—evergreen species*
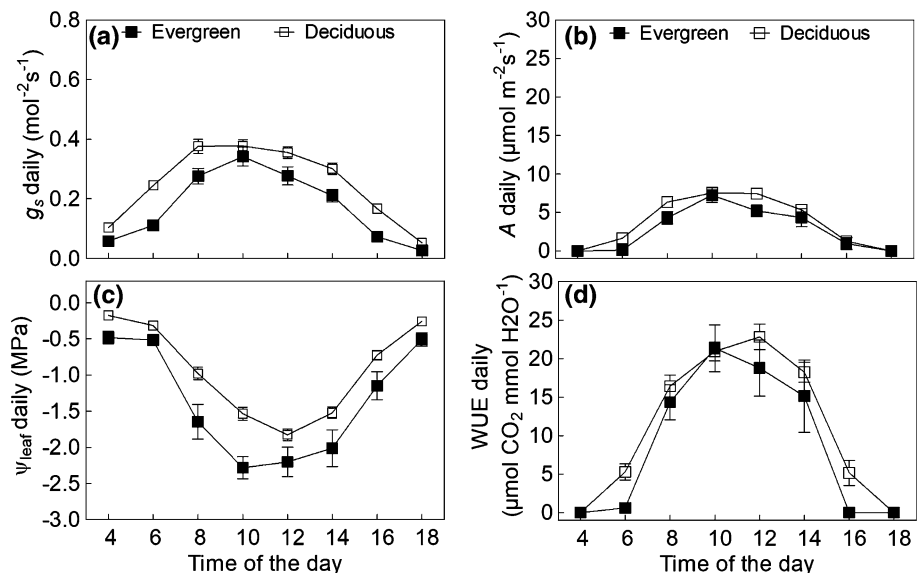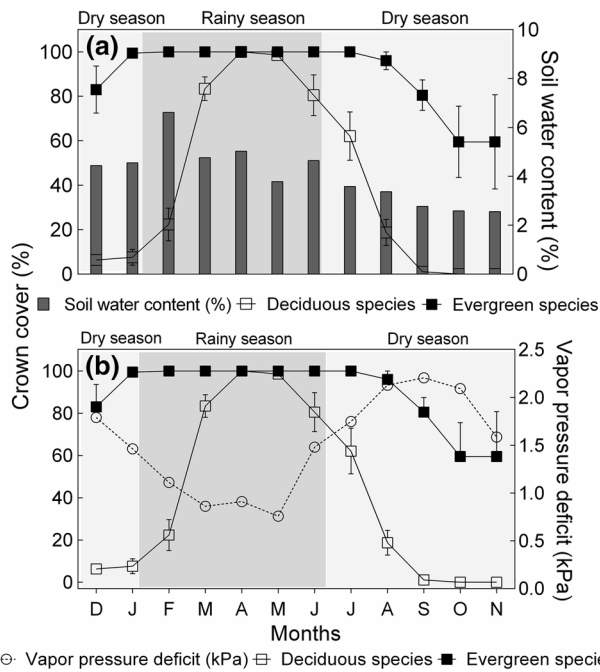
Fig. 6 Monthly variation in crown cover (%) of 17 deciduous and 5 evergreen species in relation to soil water content (SWC %; **a** and vapor deficit pressure (VPD kPa; **b** *Open square—deciduous species; closed square—evergreen species; grey bars—SWC; open circle—VPD*

Table 3 Models and R^2 values from the simple regression and multiple regression analysis of crown cover (%) in relation to soil water content (%) and vapor pressure deficit (kPa)

Model	Deciduous species (Crown cover)	P value	Evergreen species (Crown cover)	P value
SWC	0.67	0.01*	0.58	0.02*
VPD	0.69	0.006**	0.25	0.77 ns
SWC+VPD	0.86	0.0001***	0.58	0.01*

The models were denominated SWC (soil water content), VPD (vapor pressure deficit), and SWC+VPD (combines the first and second models). *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; *ns* not significant

species of seasonally dry forest of Panama, the Ψ_{xylem} of *Genipa americana* declined after leaf shedding, putting the hydraulic system at risk of failure. These authors argue that plants like *G. americana* should have mechanisms to recover hydraulic conductivity (i.e. embolism refilling or xylem production) and/or are programmed to senesce before hydraulic failure occurs (Wolfe et al. 2016).

Some deciduous species in our study with high ρ_{wood} and declining Ψ_{xylem} after leaf shedding (e.g. the fast-growing
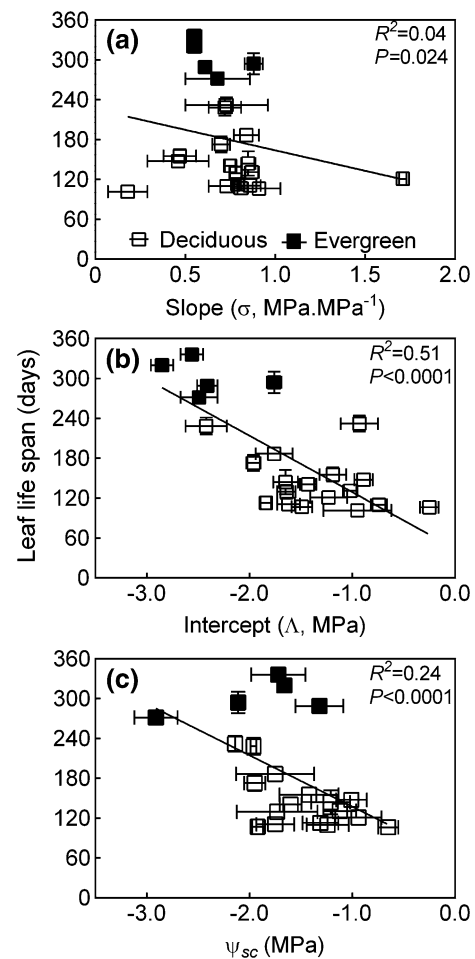

Fig. 7 Linear regression between hydraulic traits: **a** slope (σ), **b** intercept (Λ) and **c** water potential responsible for 50% stomatal closure (Ψ_{SC}) and leaf life span (LL) for 17 deciduous and five evergreen species. *Value of each species of stomatal behavior iso/anisohydric in response to drought (σ) and maximum transpiration rate per unit of water transport capacity (Λ). Average of LL and Ψ_{SC} in five individuals for specie. Open square—deciduous species; black square—evergreen species*

M. caesalpiniifolia) showed die-off of twigs, branches, and even trunks during the dry season. These parts were rapidly replaced after resprouting during a new growth phase in the following rainy season (B.C. Souza *pers. observ*). Even though we have not investigated thoroughly, the mechanisms of water acquisition and storage in the tissues, we suggest that further studies should assess the hydraulic mechanisms associated with tolerance to highly negative $\Psi_{xylemPD}$ as well as the mechanisms involved in tissue production and fast water flow recovery observed in some deciduous species. We also hypothesize that fast-growing trees in this ecosystem are more prone to hydraulic failure during drought and can recover from embolism through new xylem tissue production (Eller et al. 2018).

Fig. 8 Ordination of seven leaf and hydraulic traits on two principal component axes constructed based on average values of species traits. The factor loadings of deciduous and evergreen species on PC1 and PC2 axis are shown in (**a**) ordination of species shown in (**b**). Open circle—deciduous species; closed circle—evergreen species. The original data were standardized. *LL—Leaf lifespan; LMA—leaf dry mass per area; gs—conductance stomatal; A_m—maximum photosynthesis rate per unit mass; Ψ_{SC}—water potential responsible for 50% of stomatal closure; Λ—maximum transpiration rate per unit of water transport capacity and σ—indicator of classical stomatal behaviour iso/anisohydry in response to drought*
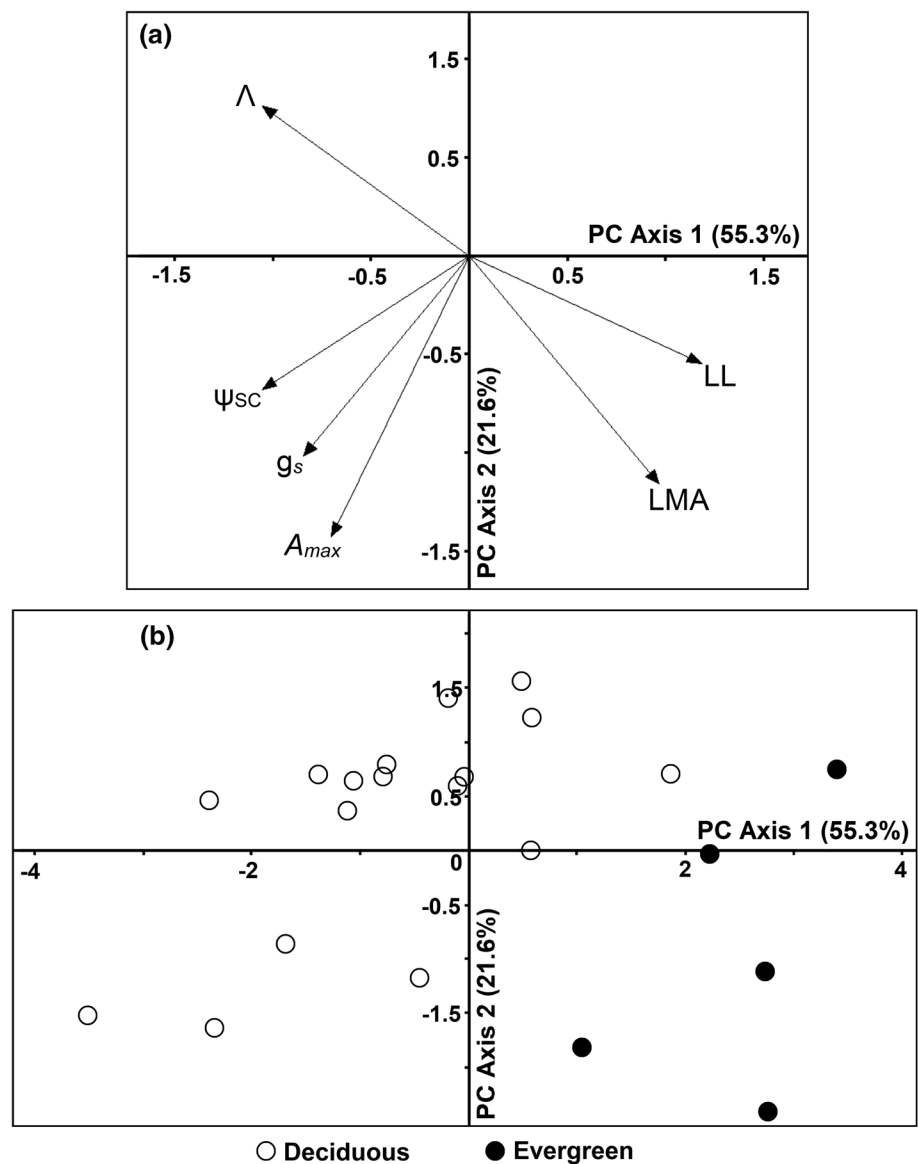
Another finding is the low variation in $\Psi_{xylemPD}$ throughout the seasons observed in some deciduous and evergreen species (except *X. americana*). For some deciduous species, low ρ_{wood} allows the maintenance of Ψ_{xylem} due to their high-water storage capacity in the stem (Borchert 1994; Borchert and Rivera 2001; Choat et al. 2005; Chen et al. 2009; Lima and Rodal 2010; Lima et al. 2012; Oliveira et al. 2015). Evergreen species have high ρ_{wood} with low capacity to store water (*see* Borchert 1994; Borchert and Rivera 2001; Lima and Rodal 2010; Lima et al. 2012; Oliveira et al. 2015) and yet maintain the Ψ_{xylem} slightly variable. Although wood density (ρ_{wood}) is a functional trait that predicts the capacity to regulate the seasonal water status for deciduous species, we hypothesize that rooting depth may be an important trait

influencing the water status in evergreen species (Brum et al. 2017; Oliveira et al. 2014).

Finally, we showed that key hydraulic traits (Λ and Ψ_{SC}) are strongly associated to leaf phenology. The intercept (Λ) of the relation between Ψ_{PD} and Ψ_{MD} represents the maximum transpiration rate per unit of water transport capacity or, equivalently, the capacity of the plant (leaf pressure drops Ψ_{leaf}) to 'pull' water when there is plenty available in the soil (Martínez-Vilalta et al. 2014). The Ψ_{SC} reflects the species ability to control evaporative demand and to adjust to changes in water availability during the rainy season (Brodribb et al. 2003). Therefore, the relationship between Λ and Ψ_{SC} and leaf phenology suggests that deciduous are less tolerant to drought than evergreen species, which have more negative stem water potentials that allow higher water

absorption by the roots and stomata closure at more negative thresholds (Klein 2014; Martínez-Vilalta et al. 2014). Future research should explore how differences in stomatal sensitivity affect carbon gain in species with contrasting leaf phenology.

References

Ackerly D (2004) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. Ecol Monogr 74:25–44. https://doi.org/10.1890/03-4022

Ahlström A, Raupach MR, Schurgers G et al (2015) The dominant role of semi-arid ecosystems in the trend and variability of the land CO2 sink. Science 348:895–899. https://doi.org/10.1002/2015JA021022

Allen SE, Grimshaw HM, Parkinson JA, Quarmby CL (1974) Chemical analysis of ecological materials, 1st edn. Blackwell Scientific Publications, Oxford, England

Araújo JC, Döll P, Güntner A, Krol M, Abreu CBR, Hauschild M, Mendiondo EM (2004) Water scarcity under scenarios for global climate change and regional development in semi-arid northeastern Brazil. Water Int 29:209–220. https://doi.org/10.1080/02508060408691770

Atkin OK, Bloomfield KJ, Reich PB, Tjoelker MG, Asner GP, Bonal D, Bönisch G, Bradford MG, Cernusak LA, Cosio EG, Creek D, Crous KY, Domingues TF, Dukes JS, Egerton JJG, Evans JR, Farquhar GD, Fyllas NM, Gauthier PPG, Gloor E, Gimeno TE, Griffin KL, Guerrieri R, Heskel MA, Huntingford C, Ishida FY, Kattge J, Lambers H, Liddell MJ, Lloyd J, Lusk CH, Martin RE, Maksimov AP, Maximov TC, Malhi Y, Medlyn BE, Meir P, Mercado LM, Mirotchnick N, Ng D, Niinemets Ü, O'Sullivan OS, Phillips OL, Poorter L, Poot P, Prentice IC, Salinas N, Rowland LM, Ryan MG, Sitch S, Slot M, Smith NG, Turnbull MH, Vanderwel MC, Valladares F, Veneklaas EJ, Weerasinghe LK, Wirth C, Wright IJ, Wythers KR, Xiang J, Xiang S, Zaragoza-Castells J (2015) Global variability in leaf respiration in relation to climate, plant functional types and leaf traits. New Phytol 206:614–636. https://doi.org/10.1111/nph.13253

Blomberg SP, Garland T, Ives AR (2003) Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. Evolution (N Y) 57:717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Bonan GB, Levis S, Sitch S, Vertenstein M, Oleson KW (2003) A dynamic global vegetation model for use with climate models: concepts and description of simulated vegetation dynamics. Glob Chang Biol 9:1543–1566. https://doi.org/10.1046/j.1529-8817.2003.00681.x

Borchert R (1994) Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology 75:1437–1449. https://doi.org/10.2307/1937467

Borchert R, Rivera G (2001) Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. Tree Physiol 21:213–221. https://doi.org/10.1093/treephys/21.4.213

Borchert R, Rivera G, Hagnauer W (2002) Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. Biotropica 34:27–39. https://doi.org/10.1646/0006-3606(2002)034[0027:movpia]2.0.co;2

Bremner JM (1965) Total Nitrogen. Methods of soil analysis Part 2 - Chemical and Microbiological Properties, number 9 in the series Agronomy. American Society of Agronomy, Inc., Publisher USA

Brodribb TJ, Holbrook NM (2005) Leaf physiology does not predict leaf habit; examples from tropical dry forest. Trees 19:290–295. https://doi.org/10.1007/s00468-004-0390-3

Brodribb TJ, Holbrook NM, Edwards EJ, Gutiérrez MV (2003) Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. Plant Cell Environ 26:443–450. https://doi.org/10.1046/j.1365-3040.2003.00975.x

Brodribb TJ, Holbrook NM, Gutiérrez MV (2002) Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees. Plant Cell Environ 25:1435–1444. https://doi.org/10.1046/j.1365-3040.2002.00919.x

Brum M, Teodoro GS, Abrahão A, Oliveira RS (2017) Coordination of rooting depth and leaf hydraulic traits defines drought-related strategies in the campos rupestres, a tropical montane biodiversity hotspot. Plant Soil 420:467–480. https://doi.org/10.1007/s11104-017-3330-x

Bucci SJ, Goldstein G, Meinzer FC, Franco AC, Campanello P, Scholz FG (2005) Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plant water potential in Neotropical savanna trees. Trees 19:296–304. https://doi.org/10.1007/s00468-004-0391-2

Bucci SJ, Goldstein G, Meinzer FC, Franco AC, Campanello P, Scholz FG (2004) Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plant water potential in Neotropical savanna trees. Trees 19:296–304. https://doi.org/10.1007/s00468-004-0391-2

Buckley TN (2005) The control of stomata by water balance. New Phytol 168:275–291. https://doi.org/10.1111/j.1469-8137.2005.01543.x

Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. Annu Rev Ecol Syst 13:229–259. https://doi.org/10.1146/annurev.es.13.110182.001305

Chen JW, Zhang Q, Cao KF (2009) Inter-species variation of photosynthetic and xylem hydraulic traits in the deciduous and evergreen Euphorbiaceae tree species from a seasonally tropical forest in south-western China. Ecol Res 24:65–73. https://doi.org/10.1007/s11284-008-0482-4

Choat B, Ball MC, Luly JG, Donnelly CF, Holtum JAM (2006) Seasonal patterns of leaf gas exchange and water relations in dry rain forest trees of contrasting leaf phenology. Tree Physiol 26:657–664. https://doi.org/10.1093/treephys/26.5.657

Choat B, Ball MC, Luly JG, Holtum JAM (2005) Hydraulic architecture of deciduous and evergreen dry rainforest tree species from north-eastern Australia. Trees 19:305–311. https://doi.org/10.1007/s00468-004-0392-1

Coste S, Baraloto C, Leroy C, Marcon É, Renaud A, Richardson AD, Roggy JC, Schimann H, Uddling J, Hérault B (2010) Assessing foliar chlorophyll contents with the SPAD-502 chlorophyll meter: a calibration test with thirteen tree species of tropical rainforest in French Guiana. Ann For Sci 67:607. https://doi.org/10.1051/forest/2010020

Damesin C, Rambal S, Joffre R (1998) Co-occurrence of trees with different leaf habit: a functional approach on Mediterranean oaks. Acta Oecologica 19:195–204. https://doi.org/10.1016/S1146-609X(98)80024-6

Eamus D (1999) Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. Trends Ecol Evol 14:11–16. https://doi.org/10.1016/S0169-5347(98)01532-8

Eller CB, Barros FV, Bittencourt PRL et al (2018) Xylem hydraulic safety and construction costs determine tropical tree growth. Plant Cell Environ 41:548–562. https://doi.org/10.1111/pce.13106

Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. Evolution (N Y) 39:783–791. https://doi.org/10.1111/j.1558-5646.1985.tb00420.x

Fournier LA (1974) Un método cuantitativo para la medición de características fenológicas en árboles. Turrialba 24:422–423

Fu PL, Jiang YJ, Wang AY, Brodribb TJ, Zhang JL, Zhu SD, Cao KF (2012) Stem hydraulic traits and leaf water-stress tolerance are co-ordinated with the leaf phenology of angiosperm trees in an Asian tropical dry karst forest. Ann Bot 110:189–199. https://doi.org/10.1093/aob/mcs092

Gleason SM, Westoby M, Jansen S, Choat B, Hacke UG, Pratt RB, Bhaskar R, Brodribb TJ, Bucci SJ, Cao K, Fan Z, Feild TS, Jacobsen AL, Johnson DM, Domec J, Mitchell PJ, Morris H, Nardini A, Pittermann J, Schreiber SG, Sperry JS, Wright IJ, Zanne AE (2015) Weak tradeoff between xylem safety and xylem- specific hydraulic efficiency across the world's woody plant species. New Phytol 209:123–136. https://doi.org/10.1111/nph.13646

Goldstein G, Rada F, Rundel P, Azocar A, Orozco A (1989) Gas exchange and water relations of evergreen and deciduous tropical savanna trees. Ann des Sci For 46:448–453. https://doi.org/10.1051/forest:198905art0100

Hasselquist NJ, Allen MF, Santiago LS (2010) Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence. Oecologia 164:881–890. https://doi.org/10.1007/s00442-010-1725-y

Holbrook NM, Whitbeck JL, Mooney HA (1995) Drought responses of neotropical dry forest trees. In: Bullock SH, Mooney HA, Medina E (eds) Seasonally Dry Tropical Forests, 1st edn. Cambridge University Press, New York, pp 243–276

IPCC (2015) Intergovernmental Panel On Climate Change. Climate change (2014) mitigation of climate change, 1st edn. Cambridge University Press, Cambridge, United Kingdom

Ishida A, Diloksumpun S, Ladpala P, Staporn D, Panuthai S, Gamo M, Yazaki K, Ishizuka M, Puangchit L (2006) Contrasting seasonal leaf habits of canopy trees between tropical dry-deciduous and evergreen forests in Thailand. Tree Physiol 26:643–656. https://doi.org/10.1093/treephys/26.5.643

Ishida A, Harayama H, Yazaki K, Ladpala P, Sasrisang A, Kaewpakasit K, Panuthai S, Staporn D, Maeda T, Gamo M, Diloksumpun S, Puangchit L, Ishizuka M (2010) Seasonal variations of gas exchange and water relations in deciduous and evergreen trees in monsoonal dry forests of Thailand. Tree Physiol 30:935–945. https://doi.org/10.1093/treephys/tpq025

Jackson RB, Mooney HA, Schulze E-D (1997) A global budget for fine root biomass, surface area, and nutrient contents. Proc Natl Acad Sci 94:7362–7366. https://doi.org/10.1073/pnas.94.14.7362

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO (2010) Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Klein T (2014) The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. Funct Ecol 28:1313–1320. https://doi.org/10.1111/1365-2435.12289

Kröber W, Heklau H, Bruelheide H (2015) Leaf morphology of 40 evergreen and deciduous broadleaved subtropical tree species and relationships to functional ecophysiological traits. Plant Biol 17:373–383. https://doi.org/10.1111/plb.12250

Levitt J (1980) Responses of Plants to Environmental Stresses, 2nd edn. Academic Press, New York

Lima ALA, Rodal MJN (2010) Phenology and wood density of plants growing in the semi-arid region of northeastern Brazil. J Arid Environ 74:1363–1373. https://doi.org/10.1016/j.jaridenv.2010.05.009

Lima ALA, Sampaio EVSB, Castro CC, Rodal MJN, Antonino ACD, Melo AL (2012) Do the phenology and functional stem attributes of woody species allow for the identification of functional groups in the semiarid region of Brazil? Trees 26:1605–1616. https://doi.org/10.1007/s00468-012-0735-2

Lima TRA, Carvalho ECD, Martins FR, Oliveira RS, Miranda RS, Pereira L, Bittencourt PRL, Sobczak JCMSM, Costa RC, Araújo FS (2018) Lignin composition is related to xylem embolism resistance and leaf life span in trees in a tropical semiarid climate. New Phytol 219:1252–1262. https://doi.org/10.1111/nph.15211

Marengo JA, Alves LM, Soares WR, Rodriguez DA, Camargo H, Riveros MP, Pabló AD (2013) Two contrasting severe seasonal extremes in tropical South America in 2012: Flood in Amazonia and drought in Northeast Brazil. J Clim 26:9137–9154. https://doi.org/10.1175/JCLI-D-12-00642.1

Marengo JA, Bernasconi M (2015) Regional differences in aridity/drought conditions over Northeast Brazil: present state and future projections. Clim Change 129:103–115. https://doi.org/10.1007/s10584-014-1310-1

Marengo JA, Jones R, Alves LM, Valverd MC (2009) Future change of temperature and precipitation extremes in South America as derived from the PRECIS regional climate modeling system. Int J Climatol 29:2241–2255. https://doi.org/10.1002/joc.1863

Markesteijn L, Poorter L (2009) Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. J Ecol 97:311–325. https://doi.org/10.1111/j.1365-2745.2008.01466.x

Markesteijn L, Poorter L, Paz H, Sack L, Bongers F (2011) Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. Plant Cell Environ 34:137–148. https://doi.org/10.1111/j.1365-3040.2010.02231.x

Martínez-Vilalta J, Poyatos R, Aguadé D, Retana J, Mencuccini M (2014) A new look at water transport regulation in plants. New Phytol 204:105–115. https://doi.org/10.1111/nph.12912

McCune B, Grace JB (2002) Analysis of Ecological Communities. MjM Software Desing, Gleneden Beach

McCune B, Mefford MJ (2011) PC-ORD. Multivariate Analysis of Ecological Data. Version 6. MjM Software, Gleneden Beach, Oregon, USA

Mediavilla S, Escudero A (2003) Stomatal responses to drought at a Mediterranean site: A comparative study of co-occurring woody species differing in leaf longevity. Tree Physiol 23:987–996. https://doi.org/10.1093/treephys/23.14.987

Miyazawa Y, Kikuzawa K (2005) Winter photosynthesis by saplings of evergreen broad-leaved trees in a deciduous temperate forest. New Phytol 165:857–866. https://doi.org/10.1111/j.1469-8137.2004.01265.x

Moro MF, Lughadha EN, Araújo FS, Martins FR (2016) A Phytogeographical Metaanalysis of the Semiarid Caatinga Domain in Brazil. Bot Rev 82:91–148. https://doi.org/10.1007/s12229-016-9164-z

Moro MF, Lughadha EN, Filer DL, Araújo FS, Martins FR (2014) A catalogue of the vascular plants of the Caatinga Phytogeographical Domain: a synthesis of floristic and p. Phytotaxa 160:1–118

Münkemüller T, Lavergne S, Bzeznik B, Dray S, Jombart T, Schiffers K, Thuiller W (2012) How to measure and test phylogenetic signal. Methods Ecol Evol 3:743–756. https://doi.org/10.1111/j.2041-210X.2012.00196.x

Olivares E, Medina E (1992) Water and nutrient relations of woody perennials from tropical dry forests. J Veg Sci 3:383–392. https://doi.org/10.2307/3235764

Oliveira CC, Zandavalli RB, Lima ALA, Rodal MJN (2015) Functional groups of woody species in semi-arid regions at low latitudes. Austral Ecol 40:40–49. https://doi.org/10.1111/aec.12165

Oliveira RS, Christoffersen BO, de V. Barros F, et al (2014) Changing precipitation regimes and the water and carbon economies of trees. Theor Exp Plant Physiol 26:65–82. https://doi.org/10.1007/s40626-014-0007-1

Peel MC, Finlayson BL, McMahon TA (2007) Updated world map of the Koppen-Geiger climate classification. Hydrol Earth Syst Sci 11:1633–1644. www.hydrol-earth-syst-sci.net/11/1633/2007

Pennington RT, Lavin M, Oliveira-filho A (2009) Woody plant diversity, evolution and ecology in the tropics: perspectives from seasonally dry tropical forests. Annu Rev Ecol Evol Syst 40:437–457. https://doi.org/10.1146/annurev.ecolsys.110308.120327

Pennington RT, Prado DE, Pendry C (2000) Neotropical seasonally dry forests and quaternary vegetation changes. J Biogeogr 27:261–273. https://doi.org/10.1046/j.1365-2699.2000.00397.x

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, Steege H, Heijden MGA, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:167–234. https://doi.org/10.1071/BT12225

Powers JS, Tiffin P (2010) Plant functional type classifications in tropical dry forests in Costa Rica: leaf habit versus taxonomic approaches. Funct Ecol 24:927–936. https://doi.org/10.1111/j.1365-2435.2010.01701.x

R Development Core Team (2015) R: a language and environment for statistical computing

Reich PB, Borchert R (1982) Phenology and Ecophysiology of the Tropical Tree, Tabebuia Neochrysantha (Bignoniaceae). Ecology 63:294–299. https://doi.org/10.2307/1938945

Reich PB, Wright IJ, Lusk CH (2007) Predicting leaf physiology from simple plant and climate attributes: a global GLOPNET analysis. Ecol Appl 17:1982–1988. https://doi.org/10.1890/06-1803.1

Salazar LF, Nobre CA, Oyama MD (2007) Climate change consequences on the biome distribution in tropical South America. Geophys Res Lett 34:1–6. https://doi.org/10.1029/2007GL029695

Sampaio EVSB (1995) Overview of the Brazilian caatinga. In: Bullock SH, Mooney HA, Medina E (eds) Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge, pp 35–63

Silva JMC, Leal IR, Tabarelli M (2017) Caatinga: The Largest Tropical Dry Forest Region in South America, 1st edn. Springer International Publishing, Switzerland

Sobrado MA (1991) Cost-benefit relationships in deciduous and evergreen leaves of tropical dry forest species. Funct Ecol 5:608–616. https://doi.org/10.2307/2389479

Sobrado MA (1997) Embolism vulnerability in drought-deciduous and evergreen species of a tropical dry forest. Acta Oecologica 18:383–391. https://doi.org/10.1016/S1146-609X(97)80030-6

Thornthwaite CW (1948) An approach toward a rational classification of climate. Geogr Rev 38:55–94. https://doi.org/10.2307/210739

Tomlinson KW, Poorter L, Bongers F, Borghetti F, Jacobs L, Van Langevelde F (2014) Relative growth rate variation of evergreen and deciduous savanna tree species is driven by different traits. Ann Bot 114:315–324. https://doi.org/10.1093/aob/mcu107

Tyree MT, Cochard H, Cruiziat P, Sinclair B, Ameglio T (1993) Drought-induced leaf shedding in walnut: evidence for vulnerability segmentation. Plant, Cell Environ Environ 16:879–882. https://doi.org/10.1111/j.1365-3040.1993.tb00511.x

Vico G, Thompson SE, Manzoni S, Molini A, Albertson JD, Almeida-Cortez JS, Fay PA, Feng X, Guswa AJ, Liu H, Wilson TG, Porporato A (2014) Climatic, ecophysiological, and phenological controls on plant ecohydrological strategies in seasonally dry ecosystems. Ecohydrology 8:660–681. https://doi.org/10.1002/eco.1533

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ (2002) Phylogenies and community ecology. Annu Rev Ecol Syst 33:475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Webb CO, Ackerly DD, Kembel SW (2008) Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24:2098–2100. https://doi.org/10.1093/bioinformatics/btn358

Wolfe BT, Kursar TA (2015) Diverse patterns of stored water use among saplings in seasonally dry tropical forests. Oecologia 179:925–936. https://doi.org/10.1007/s00442-015-3329-z

Wolfe BT, Sperry JS, Kursar TA (2016) Does leaf shedding protect stems from cavitation during seasonal droughts? A test of the hydraulic fuse hypothesis. New Phytol 212:1007–1018. https://doi.org/10.1111/nph.14087

Worbes M, Blanchart S, Fichtler E (2013) Relations between water balance, wood traits and phenological behavior of tree species from a tropical dry forest in Costa Rica - a multifactorial study. Tree Physiol 33:527–536. https://doi.org/10.1093/treephys/tpt028

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornellssen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets Ü, Oleksyn J, Osada H, Poorter H, Pool P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821–827. https://doi.org/10.1038/nature02403