Why is liana abundance low in semiarid climates?

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Abstract Lianas are abundant in seasonal tropical forests, where they avoid seasonal water stress presumably by accessing deep-soil water reserves. Although lianas are favoured in seasonal environments, their occurrence and abundance are low in semiarid environments. We hypothesized that lianas do not tolerate the great water shortage in the soil and air characteristic of semiarid environments, which would increase the risk of embolism. We compared the rooting depth of coarse roots, leaf dynamics, leaf water potential (ψ_{leaf}), embolism resistance (P_{50}) and lethal levels of embolism (P_{88}) between congeneric lianas that occur with different abundances in two semiarid sites differing in soil characteristics and vapour pressure deficit in the air (VPD_{air}). Regardless of soil texture and depth, water availability was restricted to the rainy season. All liana species were drought deciduous and had superficial coarse roots (not deeper than 35 cm). P_{50} varied from −1.8 to −2.49 MPa, and all species operated under narrow safety margins against catastrophic (P_{50}) and irreversible hydraulic failure (P_{88}), even during the rainy season. In short, lianas that occur in semiarid environments have lower resistance to cavitation and limit carbon fixation to the rainy season because of leaf fall in the early dry season. We suggest that leaf shedding and shallow roots impairing carbon gain and growth in the dry season may explain why liana abundance is lower in semiarid than in other seasonally dry environments.

Key words: cavitation vulnerability, drought resistance, leaf fall, leaf water potential, root system.

INTRODUCTION

Mechanistic explanations for liana distribution and abundance suggest that high seasonality and low rainfall favour this growth form (Schnitzer 2005; Swaine & Grace 2007; DeWalt *et al.* 2010; Schnitzer & Bongers 2011). Considering data from 69 widely distributed tropical forests, Schnitzer (2005) showed that liana abundance is negatively correlated with annual average total rainfall and positively correlated with seasonality. To explain his findings, Schnitzer (2005) proposed that the deep roots and efficient vascular system of lianas would allow them to suffer less water stress and continue to grow in the dry season. These traits can enable lianas to fix high quantities of carbon even in the dry season and render them better competitors than other growth forms under conditions of low rainfall or water deficit (Cai *et al.* 2009; Zhu & Cao 2009). As a consequence, lianas are more abundant in climates with seasonal rainfall.

Although liana abundance increases with seasonality, Schnitzer (2005) reported that in very dry forests with average annual rainfall below 800 mm, the abundance

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of lianas is lower than in other environments. He went on to speculate that lianas do not tolerate the soil water stress and high vapour pressure air deficit in these environments. Although this pattern is consistent (DeWalt *et al.* 2010; Schnitzer & Bongers 2011), some studies showed that the average abundance of lianas in very dry forests (500–800 mm mean total annual rainfall) is similar to that found in seasonal forests with annual rainfall between 1000 and 1900 mm (Gentry 1991; Phillips & Miller 2002).

This mechanistic explanation of the pattern of liana distribution and abundance has rarely been tested (Andrade *et al.* 2005; Cai *et al.* 2009; Johnson *et al.* 2013). Studies have frequently assessed differences in drought resistance and carbon fixation between lianas and trees to explain liana abundance in seasonally dry forests (Zhu & Cao 2009; van der Sande *et al.* 2013). Some studies showed that lianas do not have a deep root system and that their hydraulic efficiency is similar to that of trees (Andrade *et al.* 2005; Johnson *et al.* 2013). Hence, the mechanisms that restrict liana distribution and abundance in very dry environments remain controversial.

The establishment and survival of plants in seasonally dry environments are related to drought resistance mechanisms (Poorter & Markesteijn 2008). Plants in these environments form a continuum of hydraulic variation from tolerance to avoidance. Drought-tolerant species have mechanisms that reduce water loss, such

as low stomatal conductance (Maherali *et al.* 2006) and a hydraulic system resistant to cavitation (Choat *et al.* 2005). Drought-avoiding species can shed leaves (Borchert 1994; Worbes *et al.* 2013) or have deep root systems (Andrade *et al.* 2005; Markesteijn & Poorter 2009). Leaf deciduousness is considered a key trait allowing drought avoidance because it decreases transpiration and the risks of hydraulic failure in the xylem during periods of water deficit (Borchert 1994; Poorter & Markesteijn 2008; Worbes *et al.* 2013). In addition, deep root systems can increase water absorption capacity in the deepest soil layers (Oliveira *et al.* 2005; Markesteijn & Poorter 2009; Oliveira *et al.* 2014), which keeps leaf water potential less negative and decreases the risk of embolism formation in the xylem. Hence, the study of a suite of key hydraulic traits that enhance plant performance under drought can be useful to understanding patterns of liana occurrence and abundance in very dry environments.

Schnell (1961) highlighted the reduced liana abundance in semiarid regions, in particular in the Brazilian semiarid tropical zone. This zone lies near the equator, between 3°–17° south latitude and 35–46° west longitude, where temperature is high throughout the year, averaging 28 °C, causing high potential evapotranspiration (PET) (1200–1800 mm year^{-1}), often more than double the total annual rainfall (Reddy 1983). The vegetation covering most of this semiarid region is denominated *caatinga* (dry thorny woodland) and occurs in areas with shallow, clayey soils, at altitudes between 300 and 500 m a.s.l. with an average annual rainfall of 700 mm (Araújo *et al.* 2011). However, in the same climatic domain, but at higher altitudes, there are other vegetation types, such as dry shrubland on deep Arenosol, where lianas are more abundant (e.g. Araújo & Martins 1999). These dry shrublands are locally called *carrasco* and occur in dystrophic, sandy deep soils with free drainage around 700 m a.s.l. with mean total annual rainfall of 900 mm (Araújo *et al.* 2011). This regional variation in liana abundance makes the Brazilian semiarid region a good model to investigate which morphological and physiological characteristics restrict the occurrence of lianas in seasonally dry environments.

Our objective was to evaluate the key hydraulic traits and phenological characteristics of lianas that might explain their occurrence and abundance in semiarid environments, that is, at the driest threshold of their distribution. We compared hydraulic architecture, coarse root depth, seasonal leaf dynamics and diurnal cycles of water potential, stomatal conductance and transpiration between congeneric liana species with contrasting abundances that occur in two vegetation types (dry shrubland in deep, sandy soil and dry thorny woodland in shallow, clayey soil) in the semiarid climate of north-eastern Brazil. We expected the following: (i) lianas that occur in a semiarid site should exhibit strong similarity in hydraulic characteristics, with an efficient water system, little resistance to drought and deep roots, as proposed by Schnitzer (2005), and (ii) strong stomatal regulation and modulation of crown leaf area would be an important strategy to deal with drought, which would be associated with seasonal soil water stress and increased vapour pressure deficit in the air (VPD_{air}).

MATERIAL AND METHODS

Study area and species

Our study was carried out in two tropical seasonally dry areas in the semiarid region of north-eastern Brazil. Both areas belong to the Serra das Almas Private Natural Heritage Reserve (5°15′00′S and 40°15′00′W), located in the southern part of the Ibiapaba Plateau, within the municipalities of Crateús, state of Ceará, and Buriti dos Montes, state of Piauí. The regional climate is Köppens's BSh hot semiarid (Sparovek *et al.* 2007).

The geomorphology of the areas comprises two units: the low-altitude (300–400 m a.s.l.) crystalline basement complex, with a flat to slightly undulating relief, and the eastern edge of the Meio Norte sedimentary basin, within the Ibiapaba Plateau, with altitudes from 500 to 700 m a.s.l. (Souza 1988). These geomorphological, pedological and altitudinal differences enable the occurrence of three vegetation types: dry thorny woodland, dry shrubland and dry forest (Araújo *et al.* 2011).

The lowland site has a shallow Leptosol (FAO 2006) with high clay content and a dense sub-superficial horizon that renders water drainage difficult. The soil is relatively rich in organic matter, nitrogen and phosphorus (Table 1). The average annual rainfall is 752 mm, and the average temperature is 28 °C (FUNCEME 2013; historical data of 1963–2013). Rains are concentrated in the first four months of the year, and the water deficit is high in the remaining months of the year (FUNCEME 2013; Fig. 1a). Following the procedures recommended by Thornthwaite (1948), the index of humidity (*Ih*) is 0.15, the index of aridity (*Ia*) is 59, the index of effective humidity (*Im*) is −35, the annual PET is 1812 and the potential evapotranspiration in the summer (PET_{summer}) represents less than 48% of PET. Hence, the climate is classified as DdA′a′ semiarid with little or no surplus water, mega-thermal with high PET throughout the year. The vegetation that covers this site is *caatinga*, dry thorny woodland, with trees, shrubs and a seasonally well-developed herbaceous stratum.

The highland, at about 700 m a.s.l, has a deep Arenosol (FAO 2006), with a sandy texture (Table 1) and free drainage. Soil humidity and water content are low, even at the deepest layers, because of low clay content and free drainage (Table 1). The soil is poor in nutrients (N and P) and has low organic matter content and high aluminium content (Table 1). The average annual rainfall is 914 mm, and the average temperature is 28 °C (meteorological

Table 1. Chemical parameters of soil aliquots measured at different depths in Leptosol and Arenosol in the Serra das Almas Natural Reserve, state of Ceará, north-eastern Brazil

Depth (cm)	Granulometric composition (g kg^{-1})					Humidity (g 100 g^{-1})			Nutrients			
	Coarse sand	Fine sand	Silt	Clay	Natural clay	0.033 MPa	1.5 MPa	Useful water	OM (g kg^{-1})	N (g kg^{-1})	P (mg kg^{-1})	Al^{3+} (cmol$_c$ kg^{-1})
						Leptosol soil						
0–3	374	332	194	100	25	16.05	9.66	6.39	41.17	2.40	17	0.15
3–17	421	346	168	64	28	8.35	3.43	4.92	12.31	10.67	17	0.20
17–26	409	307	197	87	49	10.68	4.57	6.11	7.96	0.49	17	0.30
26–34	390	171	208	231	116	18.03	10.49	7.54	8.69	0.47	2	0.60
						Arenosol soil						
0–4	400	473	56	71	13	6.14	5.92	0.22	26.58	1.45	7	1.25
4–12	330	593	18	59	10	4.34	3.40	0.94	18.83	0.96	15	1.30
12–22	337	525	88	50	10	4.10	3.06	1.04	10.14	0.60	12	1.10
22–32	291	624	32	53	9	4.41	3.05	1.36	7.86	0.49	6	0.90
32–59	331	564	21	84	10	4.41	2.98	1.43	7.14	0.42	25	0.85
59–88	268	613	37	82	17	4.60	2.84	1.76	6.10	0.38	9	0.70
88–115	290	571	52	87	17	4.40	2.58	1.82	4.24	0.22	4	0.60
115–150+	214	646	52	88	20	4.40	2.65	1.75	3.62	0.18	2	0.50

OM, organic matter; N, nitrogen; P, phosphorus; Al^{3+}: aluminium. +Indicates that the soil is deeper than what is described.
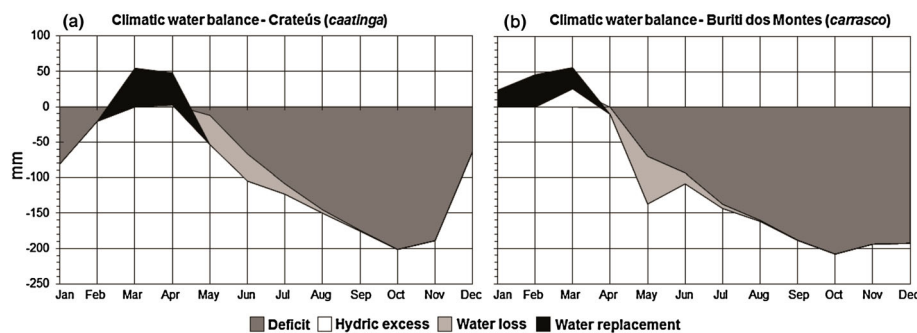
Fig. 1. Climatic water balance: (a) Caatinga, Leptosol (FUNCEME 2013, Crateús station, historical data of 1963–2013; annual rainfall: 751 mm, annual evapotranspiration: 1.811 mm, annual water deficit: 1.062 mm); (b) Carrasco, Arenosol (meteorological station of Reserva Serra das Almas; Buriti dos Montes, historical data from 2000 to 2012; annual rainfall: 914 mm, annual evapotranspiration: 2.134 mm, annual water deficit: 1.246 mm). Thornthwaite Water Balance (BHídrico GD 4.0 – 2004).

station of Serra das Almas Reserve; historical data from 2000 to 2012). In this site, the rains are also concentrated in the first four months of the year (FUNCEME 2013; Fig. 1b), $Ih = 1.22$, $Ia = 58$, $Im = -34$, $PET = 2134$ mm, $PET_{summer} < 48\%$, and the climate is also classified as DdA′a′ (Thornthwaite 1948). The vegetation that covers this type of soil is *carrasco*, a type of dense dry shrubland with emergent trees.

At each site, we delimited a 1-ha plot and recorded all liana species and their abundances. In the Leptosol site, we recorded one liana species, *Fridericia caudigera* (S. Moore) L. G. Lohmann, with 10 individuals per hectare. In the Arenosol site, we identified four liana species: *Fridericia dispar* (Bureau ex K. Schum.) L. G. Lohmann (587 individuals per hectare), *Fridericia chica* (Bonpl.) L. G. Lohmann (124 individuals per hectare), *Dioclea megacarpa* Rolfe (20 individuals per hectare) and *Cratylia mollis* Mart. ex Benth (13 individuals per hectare).

We selected the congeneric species of the family Bignoniaceae, tribe Bignonieae, genus *Fridericia*, for our study. We chose closely related species to avoid differences in hydraulic characteristics that could be influenced by phylogenetic divergence (Chen *et al.* 2009).

Abiotic variables

Soil water content – In each soil type, we opened a 1×1-m^2 ditch to install soil moisture sensors. In the Leptosol, the effective depth was only 35 cm, where we attained the bedrock. We installed dielectric soil moisture sensors ECH$_2$0, model EC-5 (Decagon Devices, Inc.) at three depths 4, 12 and 23 cm, representing horizons A, B and C. In the Arenosol, we stopped digging at 150-cm depth, although this soil type can be much deeper. We installed soil moisture sensors at 8 cm (A horizon) and 26, 68 and

135 cm (all in C horizon). Data were recorded on a HOBO data logger (Onset Computer Corporation, Bourne, MA, EUA, onset) every 15 min, from July 2011 to May 2012. Before installing the sensors, we calibrated them according to Miranda *et al.* (2007) and constructed calibrated equations for calculation of soil water content ($m^3\,m^{-3}$) for each soil type (Table 2).

The plant available water (PAW) in each soil layer was calculated, following Jipp *et al.* (1998) and Oliveira *et al.* (2005), as the difference between the amount of water measured on a given day (volumetric water content (VWC_{meas})) and the lowest value recorded during the study (VWC_{min}):

$$PAW = VWC_{meas} - VWC_{min}$$

The PAW of each soil layer was obtained by pooling PAW values at several depths. In the Leptosol, the PAW at 0–30 cm deep (PAW_{0-30}), expressed in millimetres, was calculated with the following equation: $PAW_{0-30cm} = 1000((Median\ (PAW_{4cm}, PAW_{12cm}, PAW_{23cm})/30\,cm))$, in which PAW_{4cm}, PAW_{12cm} and PAW_{23cm} represent the PAW at 4, 12 and 23 cm deep in the soil, respectively. In the Arenosol, we considered three soil layers (0- to 50-, 50- to 100- and 100- to 150-cm depths) and calculated $PAW_{0-50cm} = 1000((Median\ PAW_{8cm}, PAW_{26cm})/50)$, $PAW_{50-100cm} = 1000((PAW_{68cm})/50)$ and $PAW_{100-150cm} = 1000((PAW_{135cm})/50)$, in which PAW_{8cm}, PAW_{26cm}, PAW_{68cm} and PAW_{135cm} represent the PAW at 8, 26, 68 and 135 cm deep in the soil, respectively.

Monthly rainfall and air VPD – At each site, we recorded daily rainfall (mm), relative humidity (%)and maximum and minimum air temperatures (°C) with a micrometeorological station (HOBO Micro Station, Onset Computer Corporation, Bourne, MA, EUA). Using relative humidity and air temperature data, we calculated the air VPD (VPD_{air}) following the FAO 56 Penman–Monteith method (Allen *et al.* 1998). First, we calculated the saturation vapour pressure for maximum ($e_s(T_{max})$), average ($e_s(T_{ave})$) and minimum temperatures ($e_s(T_{min})$), with the standard equation:

$$e_s(T_{max}) = 0.6108 \star e^{\left(\frac{17.27 + T_{max}}{T_{max} + 237.3}\right)}.$$

The saturation vapour pressure ($e_s(T_{min})$) calculated using the minimum temperature (kPa) was obtained with the same equation, by substituting the value of air temperature.

We calculated atmosphere saturation vapour pressure (e_s) by summing the values $e_s(T_{max})$ and $e_s(T_{min})$ and then dividing them by two:

$$\frac{e_s = e_s\left(T_{max}\right) + e_s(T_{min})}{2}.$$

Next, we calculated the current vapour pressure (e_c) in kilopascals:

$$\frac{e_c = e_s(T_{ave})RH}{100},$$

where RH is the relative humidity (%).

With the values of e_s and e_c, we calculated the VPD_{air} with the following equation:

$$VPD = e_s - e_c.$$

Architecture and coarse root depth

To assess rooting patterns and estimate coarse root depth, we selected five adult individuals per species and carefully dug the soil around them to fully expose the roots during the beginning of the dry season (June 2013). In the Leptosol site, we could dig the roots up to 30-cm depth without damaging the plant's root system and observed the bedrock just below at 35 cm deep. In the Arenosol site, we could dig a little further than 50 cm, but we found no roots below 35-cm depth. We measured root depth with a measuring tape. We are aware that fine roots could grow deeper (e.g. Kosola *et al.* 2007), but we opted to focus on coarse roots because they set a lower limit for root growth and are much faster to measure than any methods that trace fine roots. We also adopted this procedure because of low costs and practicality, as it gives a rough estimate of coarse root depth. After digging, we collected root samples of each species to photograph and describe their morphology in the laboratory.

Leaf dynamics

From June 2011 to May 2013, we followed 10 individuals of each species fortnightly. We quantified the phenophases of adult leaf and leaf fall with the Fournier Intensity Index (Fournier 1974). With these data, we measured the duration of the crown cover.

Table 2. Equations that define the calibration curves of sensors at different depths in Leptosol and Arenosol in the Serra das Almas Natural Reserve, state of Ceará, north-eastern Brazil

Depth (cm)	Model	Equation	r^2
		Leptosol soil	
4	Linear	$\Theta = 0.8839x - 0.0107$	0.9661
12	Linear	$\Theta = 0.7036x - 0.0118$	0.964
23	Linear	$\Theta = 0.7106x - 0.0196$	0.968
		Arenosol soil	
8	Linear	$\Theta = 0.9925x - 0.1539$	0.7413
26	Linear	$\Theta = 0.7092x + 0.009$	0.9585
68	Linear	$\Theta = 0.6914x + 0.007$	0.9581
135	Linear	$\Theta = 0.6677x + 0.0051$	0.9437

Θ is soil humidity in cubic metres per cubic metre, and x is the electric potential of the sensor ECH_2O in millivolts.

Leaf water potential (ψ_{leaf}), stomatal conductance (g_s) and transpiration (E)

We measured leaf water potential (ψ_{leaf}) during the day, at 2-h intervals, from 04.00 to 18.00 hours, and selected the leaf water potential at 04.00 hours as $\psi_{predawn}$ and at 12.00 hours as ψ_{midday} in the rainy season (March 2012). The $\psi_{predawn}$ was measured using leaves wrapped in a plastic bags for at least 1 h before measurement. This procedure was necessary to reduce the night-time transpiration and allow equilibration of leaf water potential with soil water potential. The ψ_{leaf} was measured with a Scholander pressure chamber (soil moisture – Model 3005 F01). We chose healthy, fully expanded turgid leaves that did not have any of the symptoms indicative of water stress, such as those listed by Engelbrecht and Kursar (2003). We selected five individuals of each species and collected five adult leaves from them.

Simultaneously with the measurements of ψ_{leaf}, we measured stomatal conductance (g_s) and transpiration (E). The measurements were taken with an Portable Photosynthesis System (Li-Cor LI-6400XT). We used ambient conditions of temperature, CO_2 concentration and radiation. Therefore, it was not necessary to control measurement conditions in the infrared gas analyser's chamber.

Xylem vulnerability to cavitation

We built cavitation vulnerability curves for the branches using the bench-drying technique of Sperry *et al.* (1988), which is suggested by Choat *et al.* (2010) as the most appropriate method to measure vulnerability curves in species with long xylem vessels. First, we estimated the longest length of the vessels of each species using the compressed air injection technique suggested by Ewers and Fisher (1989). Maximum vessel length was 58 cm in *F. caudigera*, 63 cm in *F. dispar* and 26 cm in *F. chica*. Because of the presence of long vessels, we chose to measure the hydraulic conductivity of the branches (K_{branch}), by removing the terminal wall of the vessels. Open vessels have low hydraulic resistance, which could lead to an overestimation of the maximum conductivity (Ennajeh *et al.* 2011). Hence, we used 20-cm-long branches for all species and applied low pressure (3–4 kPa) to measure K_{branch}, which was calculated as the ratio between water mass flow and pressure gradient (Sperry *et al.* 1988).

To measure hydraulic conductivity, we collected about 30 branches of each species at dawn (between 3.00 and 5.00 hours) in the rainy season (March 2013) to minimize cavitation. The branches collected were approximately three times longer than the maximum length of vessel obtained for each species. After collection, the branches were immediately taken to the laboratory and progressively cut under water from the base up to one-third of the length, to remove any embolism from the sampling. The branches were submerged in water and covered with black plastic for 12 h for complete rehydration. Next, we began measuring initial hydraulic conductivity ($K_{initial}$) by coupling a branch to a flow meter, following Sperry *et al.* (1988). We used a potassium chloride solution (KCl 10 mmol) in filtered distilled water (Milli-Q) to maintain ionic conductivity. After measuring $K_{initial}$, we applied a water injection (*flush*) in the branches, at a constant pressure of 150 KPa for 10 min to remove embolisms. Next, we measured the maximum hydraulic conductivity (K_{max}) similarly to $K_{initial}$. The calculation of the per cent loss of conductivity (*PLC*) followed (Pammenter & Vander Willigen 1998):

$$PLC = 100 \star (K_{max} - K_{initial})/K_{max}.$$

We built cavitation vulnerability curves for each species using an exponential sigmoid function in the equation proposed by Pammenter and Willigen (1998):

$$PLC = 100/(1 + \exp(a(\psi - b))),$$

where ψ corresponds to xylem water potential, *a* is the maximum slope of the curve and *b* is the pressure in which the xylem loses 50% of hydraulic conductivity (P_{50}). We also calculated the xylem pressure inducing 88% loss of hydraulic conductivity (P_{88}), which represents the upper inflection of the curve as proposed by Choat *et al.* (2012). The P_{88} represents the ψ_{water} value corresponding to lethal levels of embolism (Choat *et al.* 2012).

In addition, we calculated hydraulic safety margins for the rainy season, using the difference between minimum water potential (ψ_{min}) and the P_{50} and P_{88} (Meinzer *et al.* 2009; Choat *et al.* 2012). The hydraulic safety margin shows the closeness between the hydraulic functioning of one species and the steepest point of the cavitation vulnerability curve for its xylem, that is, the embolism point, potentially catastrophic for the plant's hydraulic system (Johnson *et al.* 2012).

Statistical analysis

The crown area dynamics were analysed with multiple linear models. First, we tested for the occurrence of multicollinearity among explanatory variables (total monthly rainfall, VPD_{air} and PAW) using the variance inflation factor (VIF). The variables that presented VIF values above 10 were considered collinear (Borcard *et al.* 2011). The soil water content was highly correlated with total monthly rainfall and was removed from subsequent analyses. A generalized linear model (GLM) was used to compare crown cover between species and environments (Crawley 2005). Crown cover percentage was the response variable, and the total monthly rainfall and VPD_{air} were tested as explanatory variables. We assumed a quasi-Poisson error distribution (Crawley 2005). The

minimally suitable model for each species was obtained by removing non-significant terms; models were compared with an ANOVA.

Using a two-way ANOVA, we found differences in PAW between Leptosol and Arenosol. We considered the type of soil and month of the year as factors, and water content as the response variable. To test variations in ψ_{leaf}, we used a two-way ANOVA, considering species and time (predawn/midday) as factors. We analysed the cavitation vulnerability curves of the species by comparing the sum of the squares of the residues (ASQR) for the null hypothesis that the curves are coincident (Haddon 2001). All analyses were carried out in R (version 3.1.0, Core Team 2013). The significance level of 0.05 was used for all comparisons.

RESULTS

Water availability was always higher in Leptosol than in Arenosol ($P_{soil*month}$ in two-way ANOVA, $F = 21.52$, $P < 0.001$; Fig. 2a,b). In both soil types, water availability was restricted to the rainy season (Fig. 2a,b). In Arenosol, the amount of PAW was higher in the most superficial layers, between 0 and 50 cm deep (Fig. 2b).

The rooting patterns differed among species (Fig. 3a–c). *Fridericia caudigera*, which occurred in Leptosol, showed dimorphic roots, with one taproot and plagiotropic roots (Fig. 3a). The taproot grew in an orthotropic direction and reached a depth little beyond 30 cm (Fig. 3a). The plagiotropic roots grew horizontally and spread themselves up to 15 cm deep (Fig. 3a). The species that occur in Arenosol did not have dimorphic roots, but only plagiotropic roots (Fig. 3b,c). *Fridericia dispar* roots spread up to 15 cm deep, and *F. chica* up to 30 cm deep.

Regardless of site and soil type, all species had deciduous leaf phenology (Fig. 4a,b). Leaf fall in *F. caudigera* increased significantly with VPD_{air} (GLM: residual deviation: 128.13, $P = 0.002$). Total monthly rainfall had no significant effect on the maintenance of the crown area in *F. caudigera* (GLM: residual deviation: 24.68, $P = 0.146$). The maintenance of the crown area in species that occur in sites with Arenosol was explained by different factors. Leaf fall in *F. dispar* increased significantly with a drop in rainfall (GLM: residual deviation: 266.92, $P = 0.001$), whereas in *F. chica* leaf fall increased with VPD_{air} (GLM: residual deviation: 130.81, $P = 0.032$).

In the rainy season, all species showed differences between $\psi_{predawn}$ and ψ_{midday} ($P_{predawn*midday}$ in two-way ANOVA, $F = 20.37$, $P < 0.001$; Fig. 5). *Fridericia caudigera*, which occurred in Leptosol, showed $\psi_{predawn}$ around −0.5 and ψ_{midday} of −2.6 MPa (Fig. 5). *Fridericia*
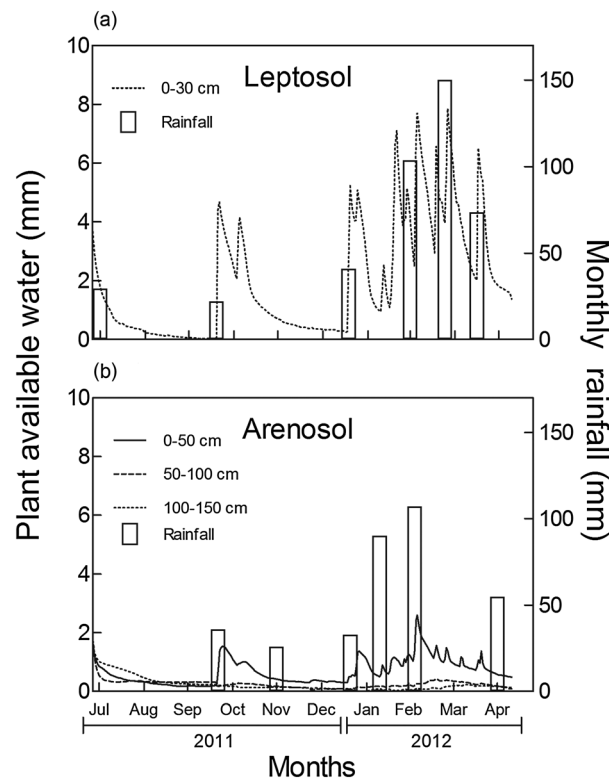
Fig. 2. Plant available water (mm) in (a) Leptosol between 0- and 30-cm depth and in (b) Arenosol at three depths, 0–50; 50–100 and 100–150 cm, in relation to monthly rainfall (mm) in each study site.
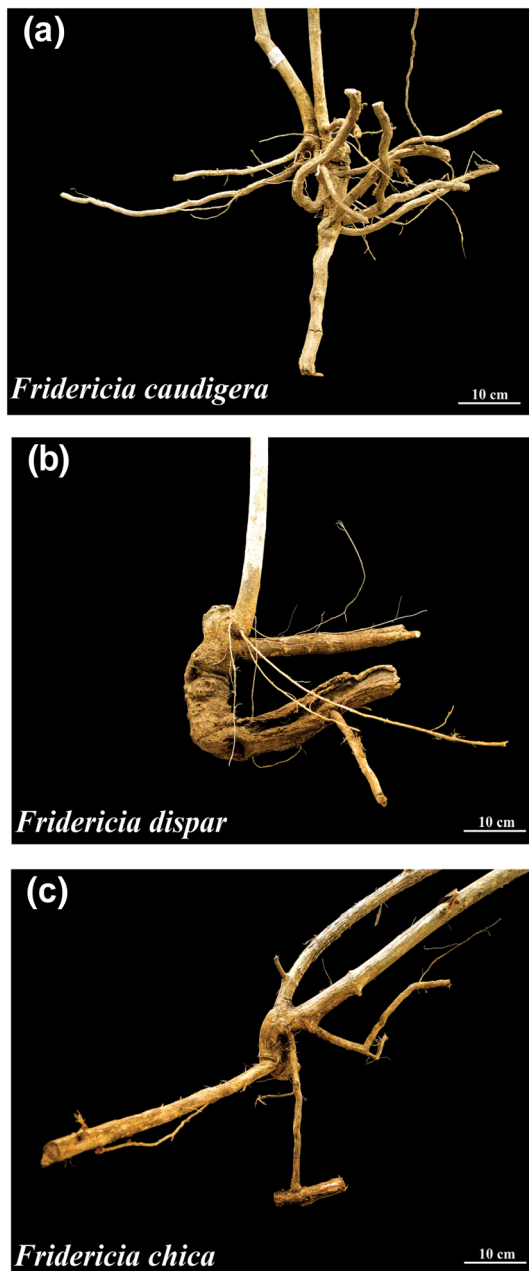
Fig. 3. Coarse root systems of (a) *Fridericia caudigera*, which occurs in Leptosol, and of (b) *Fridericia dispar* and (c) *Fridericia chica*, which co-occur in Arenosol.

dispar and *F. chica*, which co-occurred in Arenosol, showed $\psi_{predawn}$ around -0.2 and -0.35 MPa and ψ_{midday} at -1.8 and -2.3 MPa, respectively (Fig. 5). All species differed in $\psi_{predawn}$ ($F = 21.07$; $P < 0.001$; Fig. 5). *Fridericia caudigera* showed more negative values than did *F. dispar* and *F. chica* (Fig. 5). We found no difference of ψ_{midday} between *F. caudigera* and *F. chica* ($F = 2.751$; $P = 0.1336$), but both species showed more negative ψ_{midday} values than did *F. dispar* ($F = 6.606$; $P < 0.001$, $F = 3.855$; $P < 0.05$ respectively; Fig. 5).

The three species differed from each other in their cavitation vulnerability curves (ASQR, $F = 14.8722$; $P < 0.001$; Fig. 6). The cavitation vulnerability curve showed a higher slope in *F. chica* ($a = 1.107$) and lower slopes in *F. caudigera* ($a = 1.038$) and *F. dispar* ($a = 1.037$). The species with the highest xylem embolism resistance was *F. caudigera*, which lost 50% of its hydraulic conductivity (P_{50}) at a water potential of -2.49 MPa and had P_{88} of -4.22 ± 0.04 MPa (mean $\pm$ standard error; Fig. 6). *Fridericia chica* showed P_{50} at -2.09 MPa and P_{88} at -3.75 ± 0.05 MPa (Fig. 6). The lowest xylem embolism resistance was that of *F. dispar*, with P_{50} at only -1.88 MPa and P_{88} at -3.68 ± 0.07 MPa (Fig. 6).

The hydraulic safety margins in the rainy season ($\psi_{min\,rain} - P_{50}$) was higher in *F. caudigera* (+0.39). *Fridericia dispar* and *F. chica* did not show hydraulic safety margin in the rainy season, having values of 0 and -0.3, respectively. The more conservative hydraulic safety margin in the rainy season (defined as the difference between $\psi_{min\,rain}$ and P_{88}) was 1.8 MPa for *F. dispar*, 1.61 MPa for *F. caudigera* and 1.44 MPa for *F. chica*.

All species had high stomatal sensitivity to increases in transpiration during the day (Fig. 7). *Fridericia dispar* and *F. chica*, which co-occurred in the Arenosol, showed g_s and E values lower than those of *F. caudigera*, which occurred in the Leptosol (Fig. 7). These lower g_s and E values were reflected by less negative ψ_{leaf} values over the day for *F. dispar* and *F. chica* (Fig. 8). All species showed ψ_{leaf} values close to P_{50} (Fig. 8) at the day times with the greatest E and g_s. Regarding P_{88}, all species showed an average safety margin of 1.6 MPa in relation to the daily minimum ψ_{leaf} (Fig. 8).

DISCUSSION

Our results show that lianas in semiarid environments (at the driest limit of liana distribution) avoid drought and have morphological, physiological and phenological characteristics different than previously assumed (Cai *et al.* 2009; Zhu & Cao 2009; Johnson *et al.* 2013; van der Sande *et al.* 2013). Previous studies suggested that lianas have a deep root system, have high hydraulic conductivity, are evergreen, have high carbon fixation rates during the dry season and have low resistance to cavitation. However, in our semiarid site, we observed that lianas have superficial roots, are drought deciduous and, consistent with predictions, have low resistance to cavitation. These traits might negatively affect the performance of lianas in semiarid locations because they lose their ability to grow in the dry season and cannot outcompete trees. These may be one of the mechanisms that potentially explain the low
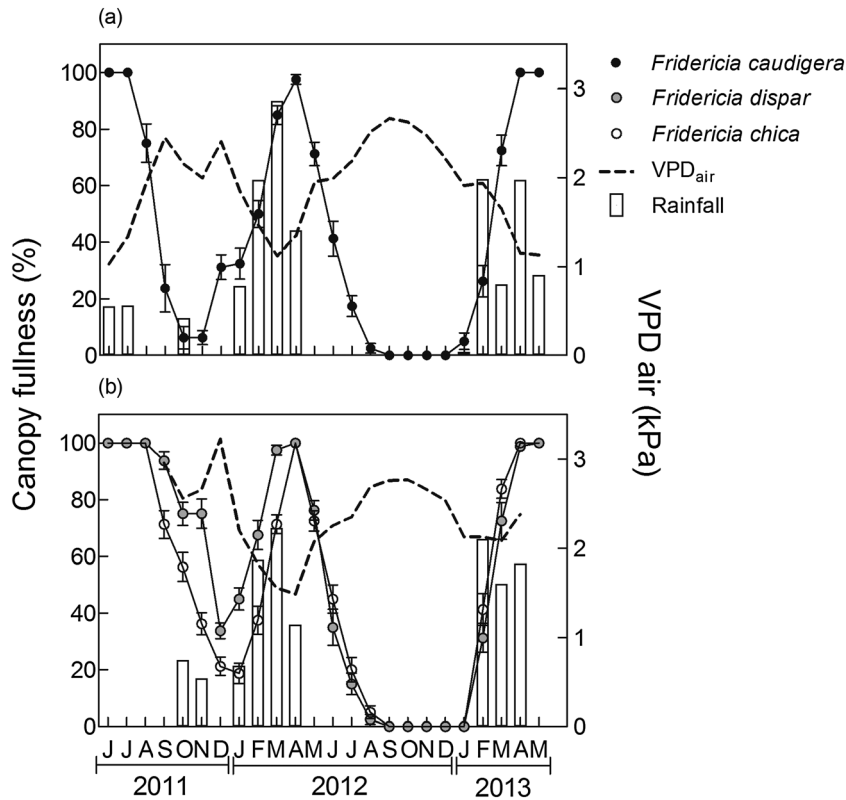
Fig. 4. Monthly average values of crown cover (%, $n = 10$), VPD_{air} (kPa) and total monthly rainfall (mm), from June 2011 to May 2013. (a) *Fridericia caudigera*, which occurs in Leptosol, and (b) *Fridericia dispar* and *Fridericia chica*, which co-occur in Arenosol.
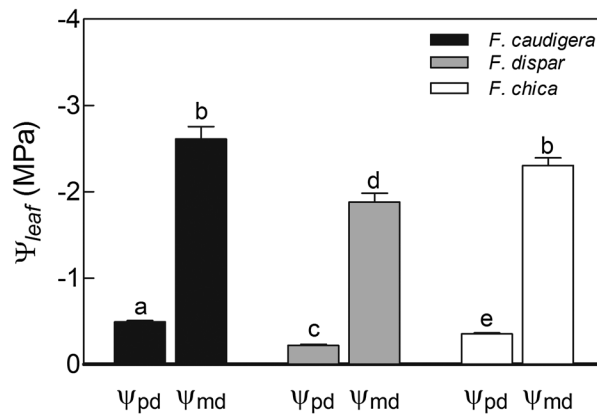

Fig. 5. Leaf water potential at predawn (ψ_{pd}) and midday (ψ_{md}) in the rainy season. Different letters show significant differences between ψ_{pd} and ψ_{md} for each species ($P < 0.05$).

richness and abundance of lianas in semiarid environments.

We noticed that regardless of the soil depth and texture and rainfall volume, water was only available only as pulses restricted to the rainy season. Although the total rainfall volume was higher in the site with Arenosol, water availability in this soil was lower than in the site with Leptosol. The sandy texture of Arenosol favours free drainage and limits water storage capacity, which reduces water availability for plants, but water retention forces are weaker than in clayey soils, meaning that while there is water in the soil, it can be relatively easily taken up by plants (FAO 2006). On the other hand, Leptosols have a high clay concentration and high water capacity, but water retention forces are stronger than in sandy soils, meaning that even when there is water in the soil, plants must develop
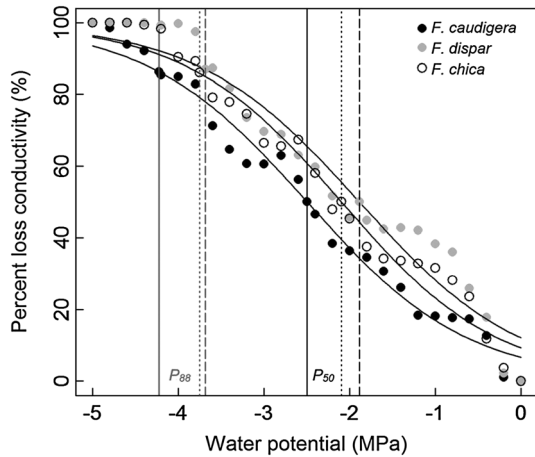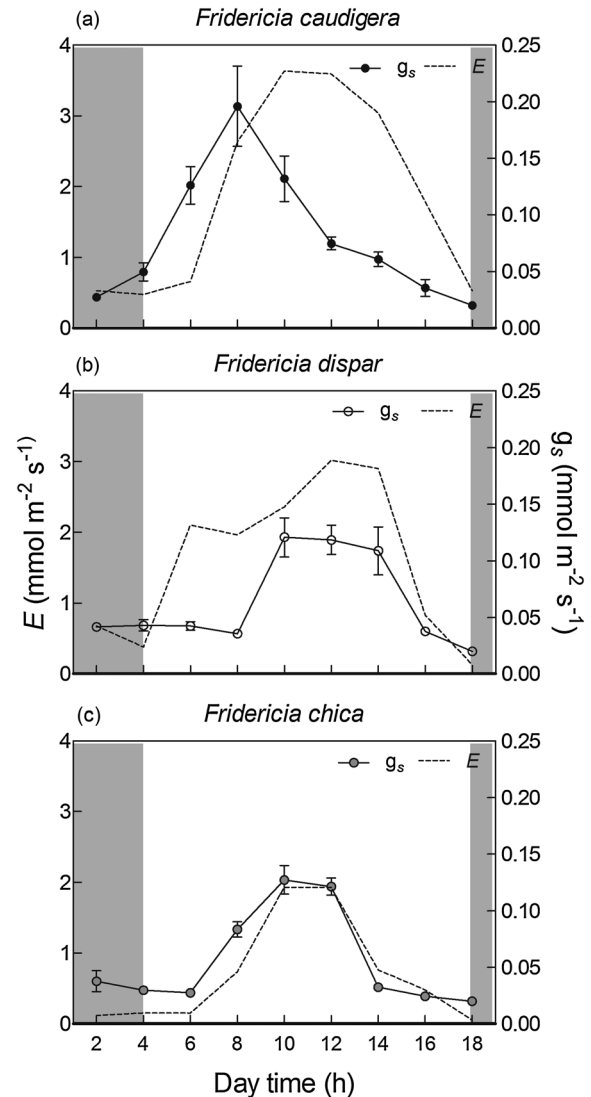
Fig. 6. Embolism vulnerability curves of *Fridericia caudigera*, which occurs in Leptosol; *Fridericia dispar* and *Fridericia chica*, which co-occur in Arenosol. Each point represents a measurement, and the percentage loss of conductivity was plotted as a function of leaf water potential. Vertical lines indicate the water potential in which there was 50% (P_{50}) and 88% (P_{88}) loss of hydraulic conductivity. Solid lines represent the P_{50} and P_{88} of the *F. caudigera*; large dashed lines represent the P_{50} and P_{88} of *F. dispar*; smaller dashed lines represent the P_{50} and P_{88} of *F. chica*. Curve parameters for the Pammenter and Vander Willigen (1998) equation: *F. caudigera* ($a = 1.038$, $b = -2.495$); *F. dispar* ($a = 1.037$, $b = -1.886$); *F. chica* ($a = 1.107$, $b = -2.095$).

more negative water potentials when taking up water (FAO 2006). As water availability in the soil is restricted to the rainy season, the species with physiological and morphological characteristics that can reduce the risk of damage by cavitation in the xylem during the period of water shortage are favoured (Choat *et al.* 2007; Zhu & Cao 2009; Lens *et al.* 2013).

Contrary to expectations, the rooting depth of lianas (coarse roots) was superficial. Several studies suggest that lianas have well-developed and deep root systems that grant access to water reserves in the soil during the dry season (Restom & Nepstad 2004; Swaine & Grace 2007). Access to deep water in the soil may decrease the risk of damages to the xylem by cavitation and may allow the maintenance of evergreen crowns and high carbon gain even during the dry season (Schnitzer 2005; Cai *et al.* 2009), which is the main competitive advantage of lianas over trees (Cai *et al.* 2009). However, the assumption of deep rooting in lianas has not been consistently investigated.

In our study, the presence of superficial roots may have been selected in these species because soil water availability is restricted to the rainy season and is higher in the more superficial layers of the soil, as Andrade *et al.* (2005) and Johnson *et al.* (2013) have

Fig. 7. Daily patterns of stomatal conductance (g_s) and transpiration (E) in the rainy season of 2012, for three congeneric liana species: (a) *Fridericia caudigera*, which occurs in Leptosol, and (b) *Fridericia dispar* and (c) *Fridericia chica*, which co-occur in Arenosol. The shading represents the period of the day without sunlight.

already suggested in studies with lianas and trees in seasonally dry environments. The factors limiting the depth of liana roots in this study seem to be different between the Leptosol and the Arenosol. In the Leptosol, the root system of *F. caudigera* could be limited by the shallow soil depth. In the Arenosol, *F. dispar* and *F. chica* do not have a main root, but only plagiotropic roots that are restricted to the soil superficial layers, where there is water in the rainy season. It is plausible that lianas in the Arenosol could access deep-soil water by means of fine roots, but we did not observe this kind of root while digging to sample the root system. In any case, we
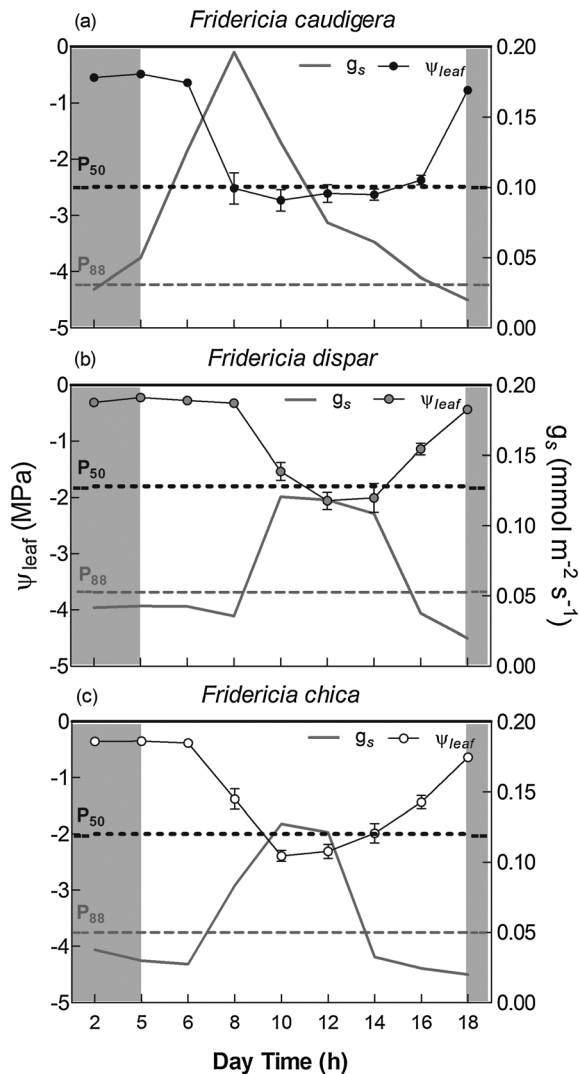
Fig. 8. Daily patterns of leaf water potential (ψ_{leaf}) in relation to stomatal conductance (g_s) in the rainy season of 2012, for three congeneric liana species: (a) *Fridericia caudigera*, which occurs in Leptosol, and (b) *Fridericia dispar* and (c) *Fridericia chica*, which co-occur in Arenosol. The shading represents the period of the day without sunlight. The dashed lines represent the water potential at which the xylem loses 50% (P_{50}) and 88% of its conductivity (P_{88}).

interpreted the deciduousness shown by all three liana species early in the dry season as a plausible indication of the shallowness of their roots systems.

Consistently with Schnitzer (2005), we observed that the lianas of semiarid environments are sensitive to soil water shortages and increases in VPD_{air} and avoid water deficits through leaf fall at the end of the rainy season, when the leaf is disconnected from the stems by means of an abscission zone (personal observations 2011–2013). Drought deciduousness is a strategy to avoid declines in stem water status

(Choat *et al.* 2006) and can reduce the risk of hydraulic failure in the xylem. Deciduousness restricts gas exchange and carbon fixation to the rainy season. Choat *et al.* (2005) and Vinya *et al.* (2013) have already recorded a similar behaviour for trees and deciduous shrubs in seasonal environments, but it is not usually described for lianas (Cai *et al.* 2009; Zhu & Cao 2009). Therefore, the lianas studied did not show a competitive advantage over trees, as they lacked a deep root system and shed leaves in the early dry season, which restricts carbon fixation and growth to the rainy season. Hence, as lianas lack their main competitive advantage in semiarid environments, we suggest that their richness and abundance should be lower in these environments than in other seasonally dry environments.

Apparently, our results showed that the studied lianas have P_{50} and P_{88} values more negative than usual (e.g. Zhu & Cao 2009; Johnson *et al.* 2013; van der Sande *et al.* 2013). However, Choat *et al.* (2010) showed that the high vulnerability to cavitation in lianas reported in previous studies was an artefact of the technique and material used. Consistently with Choat *et al.* (2010), Wheeler *et al.* (2013) provided experimental evidence that the excision of branches with native xylem pressure, even under water, results in the formation and absorption of bubbles, and consequently, the vessels are cavitated at this moment. Wheeler *et al.* (2013) proposed that diurnal cycles of vessel cavitation and recovery are rare in nature, and the plant xylem is much more resistant to cavitation than previously believed.

We also observed that the studied lianas have low hydraulic safety margin ($\psi_{min\,rain} - P_{50}$), have more conservative hydraulic safety margin ($\psi_{min\,rain} - P_{88}$) and may suffer large amounts of embolisms every day. According to Choat *et al.* (2012), it seems to be common in nature that plants have non-functional xylem portions due to embolism, despite the negative physiological impacts. Our data show that lianas are very vulnerable to xylem embolism and operate within narrow safety margins against catastrophic (P_{50}) and irreversible hydraulic failure (P_{88}). The low (or even negative) safety margins indicate that lianas experience large amounts of embolism and high risk of hydraulic failure, even during the rainy season. Several studies have suggested that lianas have efficient mechanisms to recover embolized vessels during the day (van der Sande *et al.* 2013; Johnson *et al.* 2013). However, these mechanisms are still poorly known and started being ruled out only after the study by Wheeler *et al.* (2013).

More recent studies (e.g. Knipfer *et al.* 2015; Trifilò *et al.* 2015) have contested the induction of artefact embolism evidenced by Wheeler *et al.* (2013). Using the sampling procedure of Wheeler *et al.* (2013), which assures partial relaxation of xylem pressures, Trifilò

et al. (2015) investigated diurnal changes in stem xylem embolism in nine species of dry forests and observed the occurrence of diurnal cycles of embolism formation/repair. Because of the conflicting ideas about daily cycles of embolism reverse, climbers are an important group in which to investigate the occurrence of this process, because they have a hydraulic system with low resistance to embolism, even in dry environments.

In the three lianas species studied, stomatal closure occurred at ψ_{leaf} values close to P_{50}, suggesting a coordination of stomatal closure with xylem vulnerability. The occurrence of xylem embolism might not lead to catastrophic event and might represent a hydraulic signal regulating stomatal aperture (Tombesi *et al.* 2014). Whereas stomatal regulation of transpiration can limit drops in ψ_{leaf}, the regulation of water potential prevents cavitation and embolism in the stem (Tyree & Sperry 1988; Domec & Johnson 2012). We believe that catastrophic hydraulic failures in a daily cycle should be avoided by stomatal closure in response to the increase in E, thus confirming the findings of Maherali *et al.* (2006) and Zhang *et al.* (2013). Hence, stomatal closure can regulate leaf water potential (ψ_{leaf}), which decreases xylem pressure to a range in which there is no excessive conductivity loss (Alder *et al.* 1996; Meinzer *et al.* 2009). However, accumulation of embolism during the rainy season might lead to extensive xylem dysfunction (Nardini *et al.* 2013). According to Sperry and Hacke (2002), in a seasonal cycle, leaf fall decreases xylem tensions resulting from leaf transpiration and reduces cavitation risks induced by drought stress.

Most studies comparing the hydraulic system of lianas with that of trees found high hydraulic conductivity and low resistance to cavitation in lianas (Zhu & Cao 2009; Johnson *et al.* 2013; van der Sande *et al.* 2013). Through anatomical data, Carvalho *et al.* (2015) demonstrated that the three species of lianas analysed show high potential hydraulic conductivity (K_{p}), with *F. caudigera* being the most efficient species ($16.1 \pm 3.3\,\text{kg}\,\text{m}^{-1}\,\text{MPa}^{-1}\,\text{s}^{-1}$), followed by *F. chica* ($6.79 \pm 2.7\,\text{kg}\,\text{m}^{-1}\,\text{MPa}^{-1}\,\text{s}^{-1}$) and *F. dispar* ($5.2 \pm 1.6\,\text{kg}\,\text{m}^{-1}\,\text{MPa}^{-1}\,\text{s}^{-1}$). The K_{p} shows that lianas maintain an efficient hydraulic system, and the high values of P_{50} that we found indicate a low resistance to cavitation. The most abundant species, *F. dispar* (587 individuals per hectare), which occurs in Arenosol, showed lower hydraulic safety ($P_{50} = -1.88$), whereas *F. caudigera* (10 individuals per hectare), which occurs in Leptosol, showed higher hydraulic safety ($P_{50} = -2.49$). Therefore, variations in liana abundance between Arenosol and Leptosol in semiarid environments cannot be explained only by differences in hydraulic traits.

Our findings are consistent with the pattern proposed by Schnitzer (2005), who showed that lianas with higher hydraulic efficiency and lower resistance to drought are more abundant. However, according to van der Sande *et al.* (2013), as drought resistance in lianas is low, their richness and abundance in dry environments cannot be explained by a single physiological attribute, such as P_{50}. Hence, in addition to low P_{50} values, we propose that modulation of crown area in response to increasing VPD_{air} can increase drought resistance and regulate richness and abundance of lianas in semiarid environments.

In short, we found that lianas in semiarid environments have a very efficient hydraulic system with low resistance to embolism and avoid water stress by modulating their crown area in response to decreasing soil water availability and increasing VPD_{air} in the early dry season. However, shedding leaves at the end of the rainy season/beginning of the dry season decreases carbon gain and growth during the dry season, which is the main competitive advantage of lianas over trees in more mesic environments. This could explain the low richness and abundance of lianas in plant communities receiving rainfall around 800 mm. Hence, a very efficient, but poorly resistant, hydraulic system and crown area modulation can allow lianas to live in semiarid environments, but at low abundances. Variations in liana richness and abundance among semiarid environments, such as between the *caatinga* and the *carrasco*, seem to not be explained by variations in hydraulic efficiency/safety and crown area modulation only, so we suggest that further investigations should consider other aspects of life history of lianas in semiarid environments.

ACKNOWLEDGMENTS

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