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How do leaf wetting events affect gas exchange and leaf lifespan of plants from seasonally dry tropical vegetation?

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Running head: foliar water uptake in deciduous and evergreen plants

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SUMMARY

- Foliar uptake of dew is likely an important mechanism of water acquisition for plants from tropical dry environments. However, there is still limited experimental evidence describing the anatomical pathways involved in this process and the effects of this water subsidy on the maintenance of gas exchange and leaf lifespan of species from seasonally dry tropical vegetation such as the Brazilian Caatinga.

- We performed scanning electron, bright-field and confocal microscopic analyses and used apoplastic tracers to examine the foliar water uptake (FWU) routes in four woody species with different foliar phenology and widely distributed in the Caatinga. Leaves of plants subjected to water stress were exposed to dew simulation to evaluate the effects of the FWU on leaf water potentials, gas exchange and leaf lifespan.

- All species absorbed water through their leaf cuticles and/or peltate trichomes but FWU capacity differed among species. Leaf wetting by dew increased leaf lifespan duration up to 36 days compared to plants in the drought treatment. A positive effect on leaf gas exchange and new leaf production was only observed in the anisohydric and evergreen species.

- We showed that leaf wetting by dew is relevant for the physiology and leaf lifespan of plants from seasonally dry tropical vegetation, especially for evergreen species.

INTRODUCTION

Dew formation is a common water input in seasonally dry environments (Jacobs *et al.* 1999; Agam & Berliner 2006; Pina *et al.* 2016) and can represent from 5% to 19% of all annual rainfall inputs in arid, semiarid and mesic regions (Xiao *et al.* 2009; Hanisch *et al.* 2015). In the semiarid region of Brazil, where Caatinga dryland vegetation predominates (a type of seasonally dry vegetation) (Cole 1960; Pennington *et al.* 2009; Moro *et al.* 2014; Santos *et al.* 2014), dew formation extends for up to three months after the beginning of the dry period (Pina *et al.* 2016). Dew commonly

condensates over leaf surfaces at night and this water might be directly absorbed by leaves. In fact, foliar absorption of dew is potentially an important water acquisition mechanism for plants of semiarid regions (Pina *et al.* 2016), but the prevalence of this mechanism across multiple taxa from seasonally dry tropical vegetation and its consequences for plant performance are not yet known.

Water accumulated over leaf surfaces sometimes comes at a cost for many plant functions because it reduces gas diffusion and may negatively impact gas exchange and photosynthesis (Dawson & Goldsmith 2018; Gerlein-Safdi *et al.* 2018). However, some research has demonstrated that water over leaves may be absorbed through foliar water uptake (FWU) and this process improves the leaf water status of species in tropical mesic environments (Eller *et al.* 2013, 2016; Cassana *et al.* 2016). Pina *et al.* (2016) carried out pioneering work describing FWU of dew in the Brazilian semiarid region and demonstrated that dew may be an alternative source of water for the deciduous species *Combretum leprosum* Mart. This study also describes that dew formation time in the Brazilian semiarid region lasts on average six hours (Pina *et al.* 2016). Further studies on the effect of dew regime on water status, gas exchange and leaf lifespan (the time period during which a leaf is physiologically active; LLS) of plants with contrasting foliar phenologies are needed to fully understand the role of FWU on the performance of plants in seasonally dry tropical vegetation.

The description of foliar morpho-anatomical traits and water uptake pathways is the first step to understand how the process of FWU of dew operates (Pina *et al.* 2016). There is increasing evidence, mostly from studies using apoplastic tracers, that water can be directly absorbed via leaf cuticles (Yates & Hutley 1995; Gouvra & Grammatikopoulos 2003; Limm & Dawson 2010; Xiaohua *et al.* 2016), stomata (Burkhardt 2010; Burkhardt *et al.* 2012), hydathodes (Martin & von Willert 2000) and trichomes (Eller *et al.* 2013, 2016; Martin *et al.* 2013; Pina *et al.* 2016). FWU through the cuticle can be limited during drought conditions due to contraction of the epidermis and cuticle dehydration (Limm *et al.* 2009). On the other hand, the presence of specialized structures such as trichomes and hydathodes may facilitate the occurrence of FWU (Martin & von Willert 2000; Eller *et al.* 2016; Pina *et al.* 2016). Thus, foliar anatomical studies can describe the main water entry pathways in the leaves of plants from seasonally dry tropical vegetation.

The effects of FWU can vary across species. For example, species with high FWU flux can improve the leaf water potential (Ψ_{leaf}) and absorb more water than is lost by transpiration in the same time period when compared with a species with a low FWU flux (Berry *et al.* 2018). In environments with high temperatures and high evaporation rates, stomatal regulation is also important to control leaf water balance (Buckley 2005) but little is known about the importance of FWU to maintain the leaf water balance and its relationship with stomatal regulation behavior. In general, plants exhibit a continuum of stomatal behaviors (from isohydric to anisohydric) determined by their capacity to regulate their leaf water potentials (Klein 2014; Martínez-Vilalta *et al.* 2014). Isohydric plants diminish stomatal conductance to stabilize their leaf water potential at midday (Ψ_{MD}; Klein 2014; Skelton *et al.* 2015), while anisohydric plants demonstrate high stomatal conductance and water losses even with low xylem water potentials (Klein 2014; Martínez-Vilalta *et al.* 2014; Skelton *et al.* 2015). Stomatal regulation in many species is related to other relevant physiological traits for tolerating dry conditions, such as the turgor loss point (π_{TLP}; Eller *et al.* 2016; Meinzer *et al.* 2016). Plants reduce stomata opening, gas exchange and growth when the π_{TLP} is reached (Brodribb *et al.* 2003; Blackman *et al.* 2010). In general, the stomatal behavior and π_{TLP} are associated with foliar phenology. For example, drought deciduous species tend to have low stomatal regulation (Mediavilla & Escudero 2003), less negative π_{TLP} (Bartlett *et al.* 2012) and are more sensitive to drought than evergreen species (Choat *et al.* 2006). Deciduous plants can therefore be more dependent on FWU for extending leaf function after the onset of the dry season.

Our objective was to investigate the effects of FWU on leaf water status, gas exchange and leaf lifespan of young plants of four woody species with contrasting foliar phenology from seasonally dry tropical vegetation. We hypothesized that FWU improves the leaf water status, gas exchange and increases the leaf lifespan of deciduous more than evergreen species. Additionally, climate studies predict increasing temperatures and decreasing precipitation in arid and semiarid environments such as Brazilian northeast (Sivakumar *et al.* 2005; Gornall *et al.* 2010; IPCC 2014; Marengo & Bernasconi 2015) that could negatively impact dew formation and the lifecycles of the plants growing in dry environments (Xu *et al.* 2015). Therefore, understanding how dew affects foliar ecophysiology and LLS of caatinga species will enhance the knowledge on the climate-vegetation feedbacks in dry tropical habitats.

MATERIALS AND METHODS

Species selection and site characteristics

We selected four species of contrasting leaf phenologies (early and late-deciduous and evergreen; see Oliveira *et al.* 2015; Souza *et al.* 2015): *Mimosa caesalpiniifolia* Benth. (≤ 4 months of leaf duration in natural conditions; early-deciduous), *Combretum leprosum* Mart. (≤ 7 months; late-deciduous), *Libidibia ferrea* (Mart. *ex* Tul.) L.P. Queiroz (≤ 10 months; late-deciduous) and *Cynophalla flexuosa* (L.) J. Presl (> 12 months; evergreen).

Young plants of the selected species were grown from seeds collected in the seasonally dry tropical vegetation in the *Vale do Curu* Experimental Farm (3°47'S, 39°16'W), which belongs to the Federal University of Ceará, Pentecoste, Ceará state, Brazil. Seasonally dry tropical vegetation, known locally as *caatinga*, comprises vegetation types ranging from steppic savanna to deciduous woodlands and seasonally dry tropical forests (Cole 1960; Pennington *et al.* 2009; Moro *et al.* 2014). The regional climate is dry, semiarid (type BSh following the Köppen-Geiger classification; Peel *et al.* 2007). The mean annual precipitation is 757 mm (historic mean 1973-2016), concentrated between January and May (670.9 mm), with a dry period extending from June to December (<100 mm; Funceme 2017). The mean annual temperature is 28.6 ℃ (max. 34.5 ℃ and min. 22.6 ℃), the index aridity (*Ia*) is 30.2 and annual potential evapotranspiration (PET) is 2342.8 mm.

Anatomical analyses

We used scanning electron microscopy (SEM) images of three completely expanded leaves of each species (grown under greenhouse conditions) to investigate the leaf surface morphological features that could be linked with FWU capacity. Fragments of the median vein region were fixed in a solution of paraformaldehyde and glutaraldehyde (Karnovsky 1965) and post-fixed in a 1% solution of osmium tetroxide in a sodium cacodylate buffer (0.1 M; pH 7.2). The samples were then dehydrated in an ethanol series (Johansen 1940), subjected to critical point drying (Emitech K850), metalized by gold sputtering (Emitech K550) and examined using a Model VEGA3 TESCAN (Czech Republic) scanning electron microscope.

To investigate possible FWU pathways, we analyzed fragments of the median regions of three leaves. Those fragments were fixed in a paraformaldehyde and glutaraldehyde solution (Karnovsky 1965), dehydrated in an ethanol series (Johansen 1940) and embedded in basic historesin (HistoResin, Leica Biosystems). Sections (5 µm thick) were cut using a rotary microtome (Leica 2065), mounted on slides and stained for structural analysis. We performed histochemical tests for leaf structure by staining with safranine-astra blue 9:1 (Bukatsch 1972), total lipids by staining with Sudan III (Sass, 1951) and for pectic polysaccharides by staining with ruthenium red (Johansen 1940). The results were documented using a digital camera (Leica DFC295) coupled to an optical microscope (Leica DM4000 B LED). The SEM and histological images of *C. leprosum* are available in Pina *et al.* 2016).

Apoplastic tracer experiments and leaf water absorption capacity

We exposed three undamaged and expanded leaves to the apoplastic tracer Lucifer Yellow (LY) CH (Sigma-Aldrich) for six hours (Pina *et al.* 2016) to determine the FWU pathways in each species. The leaf petioles were sealed with parafilm and the leaves held in a dark humid chamber; 100 µL of a 1% solution of the tracer was then placed on the adaxial leaf surface (Mastroberti & Mariath 2008). After six hours, the excess tracer was removed with distilled water. The leaves were then freehand sectioned, mounted on histological slides with 90% glycerol-phosphate buffer (Mastroberti & Mariath 2008) and analyzed by viewing under a LSM 710 Zeiss 710 confocal microscope (Carl Zeiss MicroImaging, GmbH) with LY emission at 550-600 nm and chlorophyll emission at 650-720 nm. On the control leaves, only distilled water was applied following the same protocol used for the apoplastic tracer. To quantify the foliar water uptake capacity, we first measured the fresh mass of five fully hydrated leaves, submerged them for 180 min in deionized water in darkness and then measured the leaf mass again. To calculate the water uptake capacity and increase in leaf water content we used the methods described by Limm *et al.* (2009).

Greenhouse dew simulation experiment

We carried out a greenhouse experiment between June and August 2016 at the Pici campus of the Federal University of Ceará, Ceará state, Brazil to investigate how dew events affect the water *status*, gas exchange and LLS of caatinga plants. The annual precipitation at the Pici campus was 1490.4 mm in 2016, concentrated between January and May (1371.3 mm), with a dry period from June to December (119.1 mm); and the mean annual temperature was 27 ℃ (max. 31.2 ℃ and min. 22.9 ℃). The vapor pressure deficit (VPD) inside the greenhouse did not vary throughout of the experiment (2.07±0.89 Kpa; P>0.05; Fig. S1). The plants were exposed to daily cycles of solar radiation (with a peak of photosynthetically active radiation (PAR) of 1092-1597 μmol $m^{-2} s^{-1}$), ambient temperature (30.75±3.53 °C) and relative humidity (52.5±8.77%).

We obtained 120 seedlings from the germination (in vermiculite) of seeds obtained from the field in 2015/2016. After the formation of the first leaf pair, the seedlings were transferred to 7-l pots that contained a 1:1 (v/v) mixture of native soil and worm humus. The pots were irrigated daily for six months to avoid water stress. At the beginning of the experiment, *M. caesalpiniifolia*, *C. leprosum*, *L. ferrea* and *C. flexuosa* plants had mean heights of 58.59±8.03 cm, 36.72±5.2 cm, 168.23±10.37 cm and 25.84±6.58 cm, respectively.

We selected 30 young individuals of each species and subjected them to the following moisture regimes: control (continuous irrigation), dew (dew simulation), and drought (complete water restriction). All plants were kept on a greenhouse bench and the plants in control treatment were watered daily while plants in the drought treatment were left to dry naturally. In the dew simulation regime, we interrupted plant irrigation in the soil and started the dew simulation only when the predawn leaf water potential (Ψ_{PD}) of each species reached its respective leaf turgor loss point (π_{TLP}).

The plants in the dew simulation regime were exposed to dew conditions daily, from 12:00 a.m. to 6:00 a.m. in a 1.5 m^2 chamber lined with impermeable transparent plastic. During the dew treatment, leaves were exposed to six continuous hours of leaf-wetting (the mean dew duration time observed in Caatinga under field conditions; Pina *et al.* 2016). The leaf-wetting was performed with the aid of an ultrasonic humidifier (Reli On). During leaf-wetting, we covered the base of the plants with parafilm and the pots with plastic to avoid any water contact with the soil, but during the day we removed the plastic and exposed the soil (Eller *et al.* 2013).

We consider that π_{TLP} represents a critical physiological point during the water stress conditions and that all species usually experience this in the field, because even during the rainy period, rainfall is erratic and seedlings commonly show signs of water stress and mortality (*see* Araújo *et al.* 2007). From this perspective, we expect dew formation to be an important water source for leaf turgor recovery in seasonally dry tropical vegetation. Therefore, we started the dew simulation experiment when species reached π_{TLP}, because at this point root uptake of water should be minimal and FWU could play a more important role. To determine the π_{TLP}, we constructed pressure-volume curves employing the induced drying method, using three completely hydrated leaves from three individuals of each species (Tyree & Hammel 1972; Bartlett *et al.* 2012).

The leaf water potentials (Ψ_{leaf}) of three plants of each species were measured for each treatment at predawn (Ψ_{PD}) and at midday (Ψ_{MD}) using a Scholander pressure chamber (Model 3005 F01, Soilmoisture Equipment Corp.). We calculated the leaf water potential difference at predawn ($\Delta\Psi_{PD}$) for each treatment using the difference between the Ψ_{PD} in intervals of five days (5-0, 10-0, 15-0 days). We used a portable infrared gas analyzer (IRGA, 6400XT, Li-Cor, Lincoln, NE, USA) to stomatal conductance (g_s) and net CO_2 assimilation rate (A) of three plants of each species for each treatment. We calculated the stomatal conductance difference (Δg_s) and net CO_2 assimilation rate difference (ΔA) for each treatment using the difference between the measurements of each parameter in intervals of five days (5-0, 10-0, 15-0 days). Mature and expanded leaves were maintained for 120 seconds in the measuring chamber; the CO_2 concentration was fixed at 400 ppm; the flow rate at 400 µmol s^{-1}; and photosynthetically active radiation at 1500 µmol m^{-2} s^{-1} (LI-6400XT LED light source). All measurements were made between 10:00 a.m. and 12:00 p.m., the period of greatest photosynthetic activity for all the species (the daily curves of A were constructed before initiating the experiments - data not shown).

We used different approaches to evaluate the stomatal regulation strategies of the species (*see* Martínez-Vilalta *et al.* 2014; Klein 2014; Lavoie-Lamoureux *et al.* 2017). However, we opted to use the approach proposed by Meinzer *et al*. (2016) which is aimed at reshaping the iso/anisohydric classification into a more biologically robust concept (Hochberg *et al*. 2018). We plot two linear regressions with Ψ_{PD} and Ψ_{MD}. In the first regression, we used only data where stomatal aperture has control over the Ψ_{MD}

(slope $\Psi_{MD}=\Psi_{PD}$). For the second regression, excluded the values to Ψ_{MD} that probably varied by irradiance, independently of Ψ_{PD}. The y-intercept of this regression is the predicted Ψ_{MD} in fully saturated soil showed a line 1:1 ($\Psi_{MD=}$ Ψ_{PD}). After this, we determined the area of a triangle bounded by the regression lines (hydroscape area; isohydric - small hydroscape area and anisohydric – large hydroscape area; Meinzer *et al.* 2016).

To evaluate the effects of FWU on the leaf lifespan (LLS), we determined the LLS of three individuals of each species per treatment. Ten leaves were marked on each of those individuals and observed daily over 60 days. The LLS are presented as the mean number of days each leaf persisted before abscising.

We also monitored the vapor pressure deficit (VPD) and the soil water content (SWC). The VPD was calculated daily, between 8:00 a.m. and 4:00 p.m., using the data collected by the humidity and air temperature sensor (MT-240, Minipa) inside the greenhouse. The SWC was determined by the gravimetric method every five days. We used three soil samples randomly chosen in pots of different experimental units of each treatment for each species (*see* Eller *et al.* 2013).

Data analysis

We used a two-way ANOVA to compare the effects of treatment and time in each specie on $\Delta\Psi_{PD}$, Δg_s and ΔA. We used as *post-hoc* tests one-way ANOVA to compare time effects into each treatment ($\alpha<0.05$). To test differences on foliar uptake capacity and increase in leaf water content between species, we used a one-way ANOVA. We used the same test to compare SWC, LLS and VPD among the treatments. The data were tested for normality and homogeneity of variance and, when necessary, log (base 10) transformed. All analyses were conducted using R v.3.3.3 software (R Core Team 2015). We used a linear regression analysis to fit the models proposed by the method described in Meinzer *et al*. (2016).

RESULTS

Leaf anatomical characteristics

We found wax crystals on the adaxial and abaxial epidermal faces of *M. caesalpiniifolia* leaves (Fig. 1a,b). The amphi-hypostomatic leaves of this species have paracytic stomata at the same level as the ordinary epidermal cells (Fig. 1b,c). The mesophyll is composed of up to two layers of palisade parenchyma and one or two layers of spongy parenchyma (Fig. 1d). The adaxial surfaces of the leaves of *M. caesalpiniifolia* showed large mucilage-containing cells (Fig. 1f). The hypostomatic leaves of *L. ferrea* (Fig. 1i) formed wax deposits in the shape of plaques and crystals on both surfaces (Fig. 1g,h) and their paracytic stomata are situated in depressions (Fig. 1h,l). The mesophyll showed a layer of palisade parenchyma and four to five spongy parenchyma layers (Fig. 1j) and the cuticle is thin (Fig. 1k). *Cynophalla flexuosa* has amphi-hypostomatic leaves and epicuticular striae next to the stomata which are located in depressions (Fig. 1m,n); its cuticle was thicker than the other species analyzed (Fig. 1q). The bifacial mesophyll is composed of two palisade parenchyma and five spongy parenchyma layers (Fig. 1o,p,r). The leaves of *C. leprosum* have two types of peltate trichomes on both surfaces. The cuticle is thin and below the epidermis, the palisade parenchyma is composed of a single layer of columnar cells. The spongy parenchyma is composed of cells with irregular sizes and shapes that become more elongated as they get closer to the abaxial surface. For more details of the foliar anatomical structure of *C. leprosum* in Pina *et al.* (2016).

Evidence of dew water uptake and absorption capacity

All species exhibit foliar water uptake capacity (FWU; Fig. 2). The control plants had only red chlorophyll auto-fluorescence and blue fluorescence of the lignified cells (Fig. 2a,c,e,g). The apoplastic tracer was absorbed through the cuticle in *M. caesalpiniifolia, L. ferrea* and *C. flexuosa* (Fig. 2b,f,h) and through the peltate trichomes in *C. leprosum* (Fig. 2d). The tracer reached the xylem in all the species, as well as the paraveinal mesophyll in *C. leprosum*. The tracer passed through all of the mesophyll and reached the abaxial epidermis in the leaves of *C. leprosum* and *C. flexuosa* (Fig. 2d,h).

Although both the deciduous and evergreen species studied had foliar uptake capacity, the deciduous *M. caesalpiniifolia* with mucilaginous epidermis cells and evergreen *C. flexuosa* showed similar and higher water uptake capacity than deciduous *C. leprosum* and *L. ferrea* (F=8.99 df. 3 P<0.001; Fig. 3a). All species showed an increase in leaf water content (LWC), however, the increase in LWC for *M. caesalpiniifolia* was even higher than other species (F=3.54 df.3 P>0.05; Fig. 3b).

Dew effects on leaf physiology and leaf lifespan

As the dew treatment was initiated after the plants reached the leaf turgor loss point (π_{TLP}), the initial soil water content (SWC) of this treatment was low and did not change over time in *M. caesalpiniifolia* (1.62±0.67%; P>0.05), *C. leprosum* (1.67±0.75%; P>0.05), *L. ferrea* (1.5±0.51%; P>0.05) and *C. flexuosa* (1.72±0.57%; P>0.05). The SWC in the drought treatment decreased over time with mean values lower than the control in all species (P<0.05).

The leaf turgor loss point (π_{TLP}) was similar for all deciduous species *M. caesalpiniifolia (*2.44±0.15), *L. ferrea* (-2.44±0.15) and *C. leprosum* (-2.62±0.22) and higher than the π_{TLP} for the evergreen species *C. flexuosa* (-2.82±0.02 MPa), indicating that the deciduous species were less drought tolerant than the evergreen species. After the measurements of the leaf water potentials of the plants of each species at predawn (Ψ_{PD}) near the respective π_{TLP}, the plants were submitted to the first dew treatment, after which the Ψ_{PD} increased to -0.76 MPa in *M. caesalpiniifolia*, -2.23 MPa in *C. leprosum*, -1.83 MPa in *L. ferrea* and -1.43 MPa in *C. flexuosa*.

The FWU increased leaf water potential at predawn (Ψ_{PD}) in the dew treatment only for *M. caesalpiniifolia* plants (Fig. 4a). The FWU was sufficient to maintain the Ψ_{PD} less negative in the dew treatment than in drought treatment for *C. leprosum* and *L. ferrea* plants (Fig. 4b,c). In *C. flexuosa*, FWU was sufficient to maintain the Ψ_{PD} close to the π_{TLP} value ($\Delta\Psi_{PD}\approx0$; Fig. 4d). Throughout the experiment, all species did not change the $\Delta\Psi_{PD}$ in the control and dew treatments (Table 1; Fig. 4). In the drought treatment, *M. caesalpiniifolia* and *C. flexuosa* showed a decrease in $\Delta\Psi_{PD}$ in the end of the experiment (Table 1; Fig. 4).

The four species showed contrasting stomatal regulation behavior (Fig. 5). The early deciduous species *M. caesalpiniifolia* is isohydric (Fig. 5a) while the late deciduous species, *C. leprosum* and *L. ferrea* showed anisohydric behavior (Fig. 5b,c). Although Despite the little temporal variation in leaf water potential (Ψ_{leaf}) for *C. flexuosa*, this species had an anisohydric stomatal behavior (Fig. 5d).

Foliar water uptake during dew simulation was not enough to allow the recovery of stomatal conductance (g_s; Fig. 6a,c,e, Table 1) and net CO_2 assimilation rate (A; Fig. 6b,d,f) for all deciduous species. However, *C. flexuosa* plants, evergreen and with an anisohydric behavior, increased g_s for 10 days and A for 15 days during dew treatment (Fig. 6g,h; Table 1).

FWU positively affected leaf lifespan (LLS; Fig.7) of all species. The LLS of the plants submitted to dew treatment was similar to control plants and higher than droughted plants (Fig. 7). FWU increased LLS by 35, 21 and 36 days in *M. caesalpinifolia*, *C. leprosum* and *L. ferrea*, respectively (Fig.7) compared to plants in drought conditions. All the *C. flexuosa* individuals in the dew treatment maintained their leaves and produced an average of nine new leaves per individual, maintaining them for more 60 days.

DISCUSSION

Our results demonstrate that foliar water uptake (FWU) occurs via trichomes and/or cuticles of both ordinary and mucilaginous epidermal cells in Caatinga species. We also demonstrate that FWU has a strong effect on leaf lifespan (LLS). All plants that received water from dew simulation over their leaf surfaces increased the LLS from 20 to 36 days compared to drought treatment plants. We provide evidence that FWU occurs in deciduous species, regardless of their stomatal regulation (iso/anisohydric behavior), but FWU did not promote recovery of their physiological functions after reaching the π_{TLP}. This result suggests that the π_{TLP} is a critical point of no physiological return for leaves of drought deciduous plants. However, the evergreen and anisohydric species, when exposed to dew, partially recovered its leaf water potential (Ψ_{leaf}) over time and increased gas exchange and production of new leaves after reaching π_{TLP}.

Pathways and capacity of foliar uptake

The young plants of *M. caesalpiniifolia*, *L. ferrea*, *C. leprosum* and *C. flexuosa* can absorb water through their leaves, as the apoplastic tracers applied to the adaxial surfaces of leaves were observed in their epidermis, mesophyll and xylem. The main anatomical route of tracer absorption in *M. caesalpiniifolia*, *L. ferrea* and *C. flexuosa* was direct diffusion through the cuticle. The tracer was observed in the trichomes and paraveinal mesophyll in *C. leprosum*, reinforcing the function of that tissue in leaf water redistribution (Pina *et al.* 2016). The absorption of the apoplastic tracer through the cuticle, mucilaginous epidermal cells and hydrophilic trichomes demonstrates the existence of different FWU pathways in plants growing in seasonally dry environments. However, these pathways are not restricted to plants of dry ecosystems, since they have been observed in plants growing in more mesic habitats (Eller *et al.* 2013, 2016).

Even though the cuticle represents an important FWU route for plants growing in semiarid environments (Riederer & Schreiber 2001), our results demonstrate that variations in leaf morphology, including the presence of hydrophilic trichomes, concentrations of plaques and wax crystals, and cuticle thickness can all affect leaf water absorption. The apoplastic tracer spread easily over the leaf surface of *M. caesalpiniifolia* (which has a thin cuticle), over *C. flexuosa* (which has a thick cuticle) and over *C. leprosum* (which has hydrophilic trichomes) (see Pina *et al.* 2016). Also, the occurrence of the epidermal cells with pectin-rich cell walls may facilitate the FWU as it increases water adsorption. Boanares *et al.* (2018) reported that species with greater FWU fluxes had more pectins in their cell walls, than those with lower rates. However, we observed that, despite the occurrence of apoplastic marker uptake in *L. ferrea*, the drop of LY tends to drip down from the leaf surface. This can be explained by the presence of plaques and wax crystals that cover the entire leaf surface (Jeffree 2006). Although the leaf cuticles are covered by waxes which can form a hydrophobic layer of long-chain aliphatic molecules (Shepherd & Griffiths 2006) and can exhibit different thicknesses, they are permeable to water (Riederer & Schreiber 2001; Oliveira *et al.* 2003), as was observed with *M. caesalpiniifolia*, *L. ferrea* and *C. flexuosa*.

Despite the observed leaf surface permeability to water in all species, the FWU capacity was higher in *M. caesalpiniifolia* and *C. flexuosa*. We suggest that the thin cuticle and mucilaginous epidermal cells amplify the FWU capacity in *M. caesalpiniifolia*. Mucilage and polysaccharides are hydrophilic compounds and

important for water adsorption (Angeles & León-Gómez 1997) and for increasing leaf water status (Robichaux & Morse 1990). Leaf water content increased ~ 20% in *M. caesalpiniifolia*, whilst in the other species it did not reach 12%, suggesting that the thicker cuticle of *C. flexuosa* does not prevent FWU. Some authors reported that cuticle is the main pathway for leaf water absorption (Yates & Hutley 1995; Gouvra & Grammatikopoulos 2003; Limm & Dawson 2010; Xiaohua *et al.* 2016), and that the thickness and chemical composition are also important to maintain leaf hydration (Oliveira *et al.* 2003). Leaf-wetting events may actually promote the occurrence of FWU, by increasing cuticle and epidermal hydration (Limm *et al.* 2009). Regardless of the leaf micro-morphology observed in studied species we observed that the exposure of leaves for six hours to water from dew simulation was enough for FWU occurs.

Dew absorption and its effects on leaf water relations and gas exchange

Here, we demonstrated that prolonged exposure of leaves to water from dew simulation enabled FWU in both deciduous and evergreen plants. Studies have demonstrated that the duration of exposure to dew is more important in terms of FWU than the quantity of water accumulated on the leaf surface (Burrage 1972; Malek *et al.* 1999; Hanisch *et al.* 2015). As such, if water availability and air humidity in dry regions diminishes, as predicted by climate change models, dew will tend to be reduced in semiarid regions (Tomaszkiewicz *et al.* 2016). In temperate monsoon forests, the reduction in dew could be more drastic and close to 70% (Xu *et al.* 2015). Therefore, reductions in dew formations in both dry and humid areas may impose more restrictive conditions for the establishment of young plants.

The increase in Ψ_{PD} observed after the first dew simulation was not maintained over time, but the FWU increased the LLS in all the species studied. Furthermore, FWU improved the Ψ_{PD} close to π_{TLP} and increased gas exchange (g_s and *A*) only in the evergreen species *C. flexuosa*. According to Eller *et al.* (2016), plants capable of absorbing water after leaf wetting events can maintain their Ψ_{PD} levels above or close to π_{TLP} over time. Similar to our observations with the deciduous species *M. caesalpinifolia*, *L. ferrea* and *C. leprosum*, Munné-bosch *et al.* (1999) demonstrated that Mediterranean area plants that could absorb dew through their leaves, increase their water *status* but not their photosynthetic capacities. We suggest that leaves of deciduous plants are more vulnerable to atmospheric drought, because when they reach

the π_{TLP}, they do not return to normal gas exchange rates. The positive effects of FWU on the evergreen species *C. flexuosa* may be associated with the hydraulic properties of its leaves which might be more embolism resistant. Foliar water uptake might be a key mechanism to the survival and establishment of evergreen species in seasonally dry tropical vegetation.

Our results indicate that for plants growing in areas with high evapotranspiration rates (>1.400mm/yr) such as seasonally dry tropical vegetation (Silva *et al*. 2011), different stomatal regulation behaviors can occur regardless of the phenological strategies, as observed for *M. caesalpinifolia*, *C. leprosum* and *L. ferrea*. The deciduous species, *M. caesalpiniifolia* is isohydric and its high FWU capacity may increase LLS and allow the recovery of leaf water status after reaching its π_{TLP}, but not of gas exchange. In other deciduous, *C. leprosum* and *L. ferrea*, the stomatal behavior was anisohydric and despite the lower FWU capacity than *M. caesalpiniifolia,* the response to the effects of FWU was similar. In general, when the plants reach the π_{TLP}, they lose their capacity to absorb water through their roots (Bartlett *et al*. 2014), reducing stomatal opening and interrupting gas exchange, independently of stomatal behavior (iso/anisohydric; Brodribb *et al*. 2003; Blackman *et al*. 2010). The π_{TLP} represents the range of Ψ_{leaf} in which species can operate before complete stomatal closure (Meinzer *et al*. 2016) and future studies should investigate the mechanisms underlying the physiological recovery capacity of leaves of *C. flexuosa* after dew exposure.

Even though FWU did not contribute to increase gas exchange in the deciduous species, it increased LLS, which may be important for the translocation of leaf resources to the branches before leaf abscission (Himelblau & Amasino 2001). On the other hand, the evergreen species *C. flexuosa* showed anisohydric behavior and the effects of FWU were relevant because they maintained the Ψ_{PD} very close to π_{TLP}, increased gas exchange, LLS and the production of new leaves. *C. flexuosa* had low stomatal regulation and FWU was important for this species and a positive effect on gas exchange. Our results suggest that species of seasonally dry ecosystem with different stomatal behaviour has high capacity of FWU (*see* Fig.3). However, a positive effect on gas exchange was only observed for the anisohydric and evergreen species. Our results corroborate the pattern observed for tropical mountane cloud forests, where plants with higher FWU capacity also had anisohydric stomatal regulation behavior (*see* Eller *et al*. 2016).

The concept or classification of iso/anisohydric has been strongly criticized and recent surveys show that different approaches classify the same species into contrasting stomatal regulation behavior (Klein 2014; Martínez-Vilalta *et al.* 2014; Martínez-Vilalta and Garcia-Forner 2017; Hochberg *et al.* 2018). For example, *C. flexuosa* shows low variation in Ψ_{PD} and Ψ_{MD} through time, even when the soil is dry, suggesting an isohydric behavior. However, this species showed a high range in the Ψ_{leaf} on a daily basis which is consistent with the anisohydric behavior (see Fig.5). According to Meinzer *et al.* (2016) the range of bidimensional variation of Ψ_{PD} and Ψ_{MD} defines the hydroscape area. The area size provides information about plant capacity to sustain stomatal activity and the Ψ_{leaf} range where the plant is able to maintain its physiological functions. Thus, species with larger hydroscapes are expected to be more anisohydric, which is the case for *C. flexuosa.*

Moreover, in a recent study Martínez-Vilalta & Garcia-Forner (2017) suggested that stomatal behaviour classification in iso/anisohydric cannot be attributed to variation in only Ψ_{leaf} because this trait is also associated with others factors such as hydraulic vulnerability and xylem embolism. Thus, other hydraulics factors such as transpiration (*E*), plant hydraulic conductance (*K*) and the difference between leaf water potential ($\Delta\Psi$) would help to classify plant hydraulic strategies and provide a more comprehensive perspective about plant hydraulic relations (Hochberg *et al.* 2018).

Contradicting our expectations, the effects of FWU on water status and gas exchange recovery was more important in evergreen than deciduous species. Deciduous species favour maximum CO_2 assimilation over a shorter LLS while evergreen species must endure higher temporal variations in water availability and foliar water uptake may be a key strategy to buffer extreme water deficits and allow the maintenance of the hydraulic integrity of leaves for longer periods in seasonally dry environments (Wright *et al.* 2004). In fact, FWU in anisohydric evergreen plants should be more significant after the rainy period, because FWU would favour the maintenance of the water status and gas exchange of those plants during the dry season.

In summary, FWU hydrates the leaf tissues and increases LLS of caatinga species. The effects of FWU on whole-plant water and carbon balance and plant survival are not yet clear and should be investigated in future studies (Berry *et al.* 2018). We conclude that in seasonally dry tropical vegetation, foliar uptake of dew water has a positive impact on the performance of evergreen plants given their low capacity for

stomatal control during drought. If global climate change produces warmer and drier conditions, with reduced dew formation (IPCC 2014; Xu *et al.* 2015), the establishment and growth of young evergreen plants, in seasonally dry tropical vegetation might be compromised.

CONCLUSION

Foliar water uptake increased leaf lifespan for all species in a seasonally dry tropical vegetation and positively affected the water status, gas exchange (g_s and *A*), production of new leaves only for the evergreen species.

AUTHOR CONTRIBUTIONS

A.A.S., A.E.R.H., F.R.M., R.S.O and R.C.C designed the research, A.E.R.H., B.C.S. and C.R.M. collected the data for the research, and A.A.S., A.E.R.H., B.C.S and E.C.D.C. analyzed the data. All authors contributed to the writing of the manuscript.

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Figures legends

Fig. 1. Scanning electron microscopy images of the leaf anatomy of *Mimosa caesalpiniifolia* (a-f), *Libidibia ferrea* (g-l) and *Cynophalla flexuosa* (m-r). (a, g, m) Adaxial Surface. (b, h, n) Stomata located on the abaxial surface. (c) Xylem (Xl), Phloem (Fl) and Stomata (St) on the central vein. (d) Adaxial epidermis (AdE), Abaxial epidermis (AbE), Chlorophyllous palisade parenchyma (Pp) and Spongy parenchyma (Sp). (e, k, q) Cuticle (Ct). (f) Mucilage (Mc). (i) Xylem (Xl), Phloem (Fl), Fibers (Fb) and Stomata (St) on the central nerve. (j) Palisade parenchyma (Pp) and Spongy parenchyma (Sp). (l) Adaxial epidermis (AdE), Abaxial epidermis (AbE) and Stomata (St). (o) Xylem (Xl), Phloem (Fl) and Fibers (Fb) on the central nerve. (p) Palisade parenchyma (Pp), Spongy parenchyma (Sp) and Stomata (St) on the abaxial face of the leaf blade. (r) Adaxial epidermis (AdE) and Abaxial epidermis (AbE).

Fig. 2. Evidence of foliar absorption through apoplastic pathways after 6 h of tracer exposure on the adaxial leaf surface of *Mimosa caesalpiniifolia* (a, b), *Combretum leprosum* (c, d), *Libidibia ferrea* (e, f) and *Cynophalla flexuosa* (g, h). (a, c, e, g) dark blue show only lignin autofluorescence of xylem of a fresh leaf (untreated leaf). (b) Apoplastic fluorescent tracer Lucifer yellow (LY) accumulation on the epidermis and in the apoplastic parenchyma pathways and xylem. (d) Presence of LY on peltate trichomes, in the apoplastic parenchyma pathways and paraveinal mesophyll. (f) LY accumulation paraveinal mesophyll. (h) Apoplastic tracer solutions applied on the adaxial surface migrated directly to the xylem, reaching the opposite leaf surface; AdE - Adaxial epidermis; AbE - Abaxial epidermis; Pp - Palisade parenchyma; Sp - Spongy parenchyma; Xy - Xylem; Tr - Trichome; Pm - Paraveinal mesophyll; AdCt - Adaxial cuticle; AbCt - Abaxial cuticle).

Fig. 3. Foliar water absorption by excised leaves of four species during submergence in deionized water for 180 min. (a) The mean (±SE) absorbed foliar water quantity standardized by leaf area. (b) The mean (±SE) % increase in leaf water content. Equal letters indicated no difference between species t-test ($\alpha = 0.05$).

Fig. 4. Temporal dynamics of the leaf water potential difference at predawn ($\Delta\Psi_{PD}$) using the difference between the Ψ_{PD} in intervals of five days in *Mimosa caesalpiniifolia* (a), *Combretum leprosum* (b), *Libidibia ferrea* (c) and *Cynophalla flexuosa* (d). All of the plants subjected to dew treatment initiated the experiments with their leaf water potential (Ψ_{leaf}) close to turgor loss point (π_{TLP}; $P>0.05$) to represent a physiological condition of maximum water stress. The error bars are the observed means ± SE. Different letters indicate statistically significant differences: uppercase between treatments and lowercase times ($P<0.05$).

Fig. 5. Classification the stomatal regulation in iso/anisohydric behavior for *Mimosa caesalpiniifolia* (a), *Combretum leprosum* (b), *Libidibia ferrea* (c) and *Cynophalla flexuosa* (d). Linear regressions with Ψ_{PD} and Ψ_{MD}, when stomatal aperture control the Ψ_{PD} (slope $\Psi_{MD}= \Psi_{PD}$) and Ψ_{MD} in fully saturated soil and its intercept with the 1:1 line ($\Psi_{MD}= \Psi_{PD}$). Red triangles represent hydroscape areas (Meinzer *et al*. 2016).

Fig. 6. Temporal dynamics of stomatal conductance difference (Δg_s) and the rate of net CO_2 assimilation difference (ΔA) using the difference between the measurements of each parameter in intervals of five days in *Mimosa caesalpiniifolia* (a, b), *Combretum leprosum* (c, d), *Libidibia ferrea* (e, f) and *Cynophalla flexuosa* (g, h). All of the plants subjected to dew treatment initiated the experiments with their leaf water potential (Ψ_{leaf}) close to turgor loss point (π_{TLP}; $P>0.05$) to represent a physiological condition of maximum water stress. The error bars are the observed means ± SE. Different letters indicate statistically significant differences: uppercase between treatments and lowercase times ($P<0.05$).

Fig. 7. Leaf lifespan (LLS) in each treatment in *Mimosa caesalpiniifolia* (a), *Combretum leprosum* (b), *Libidibia ferrea* (c) and *Cynophalla flexuosa* (d) at the end of the greenhouse experiments. The error bars are the observed means ± SE. Different letters indicate statistically significant differences between treatments ($P<0.05$).

Tables

Table 1. One-way ANOVA of the effects over time of each treatment on; leaf water potential difference at predawn ($\Delta\Psi_{PD}$), stomatal conductance difference (Δg_s), and rate of net CO_2 assimilation difference (ΔA), in *Mimosa caesalpiniifolia*, *Combretum leprosum*, *Libidibia ferrea* and *Cynophalla flexuosa*.

Supplementary files

Fig. S1. Vapor pressure deficit (VPD) inside of the greenhouse. Each box represents 50% of the observations; whiskers represent the breadth of the distribution and the cross symbol represents the mean. The same letters imply that the groups did not differ significantly ($P > 0.05$).

Table S1. Maximum stomatal conductance, maximum net CO_2 assimilation rate, leaf mass per area and absolute leaf capacitance of *M. caesalpiniifolia, L. ferrea, C. flexuosa* and *C. leprosum* submitted to three treatments of water availability (control, dew simulation and drought).
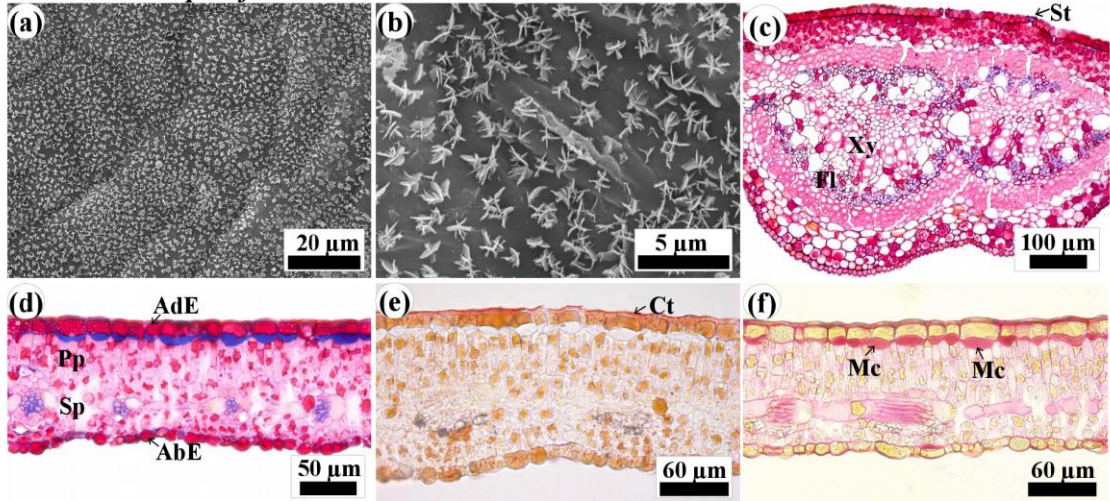
Table 1. One-way ANOVA of the effects over time of each treatment on; leaf water potential difference at predawn ($\Delta\Psi_{PD}$), stomatal conductance difference (Δg_s), and rate of net CO_2 assimilation difference (ΔA), in *Mimosa caesalpiniifolia*, *Combretum leprosum*, *Libidibia ferrea* and *Cynophalla flexuosa*.

Mimosa caesalpiniifolia

| Treatment | ANOVA | | | | Tukey HSD | | |
| | | | | | Time | | |
	Source	df	*F* value	*P* value	(5-0)x(10-0)	(5-0)x(15-0)	(10-0)x(15-0)
Control	$\Delta\Psi_{PD}$	2	0.27	0.77	0.75	0.93	0.93
	Δg_s	2	0.28	0.77	0.78	1	0.82
	ΔA	2	0	1	1	1	1
Dew	$\Delta\Psi_{PD}$	2	4.54	0.06	0.93	0.12	0.07
	Δg_s	2	0.44	0.66	0.77	0.98	0.67
	ΔA	2	1.16	0.38	0.37	0.94	0.54
Drought	$\Delta\Psi_{PD}$	2	47.38	< 0.001	< 0.05	-	-
	Δg_s	2	30.97	< 0.001	0.92	-	-
	ΔA	2	534.5	< 0.001	0.98	-	-

Combretum leprosum

| Treatment | ANOVA | | | | Tukey HSD | | |
| | | | | | Time | | |
	Source	df	*F* value	*P* value	(5-0)x(10-0)	(5-0)x(15-0)	(10-0)x(15-0)
Control	$\Delta\Psi_{PD}$	2	0.53	0.62	0.59	0.91	0.82
	Δg_s	2	0.18	0.84	0.99	0.84	0.9
	ΔA	2	0.4	0.69	0.75	0.72	1
Dew	$\Delta\Psi_{PD}$	2	0.45	0.66	0.66	0.98	0.78
	Δg_s	2	0.05	0.95	1	0.96	0.96
	ΔA	2	0	1	1	1	1
Drought	$\Delta\Psi_{PD}$	2	4.14	0.07	0.37	-	-
	Δg_s	2	129	< 0.001	0.2	-	-
	ΔA	2	78.51	< 0.001	0.93	-	-

Libidibia ferrea

| Treatment | ANOVA | | | | Tukey HSD | | |
| | | | | | Time | | |
	Source	df	*F* value	*P* value	(5-0)x(10-0)	(5-0)x(15-0)	(10-0)x(15-0)
Control	$\Delta\Psi_{PD}$	2	0.14	0.87	0.89	0.89	1
	Δg_s	2	0.07	0.94	0.94	1	0.95
	ΔA	2	0.03	0.97	0.99	0.99	0.97
Dew	$\Delta\Psi_{PD}$	2	1.38	0.32	0.45	0.34	0.97

	Source	df	F value	P value	(5-0)x(10-0)	(5-0)x(15-0)	(10-0)x(15-0)
	Δg_s	2	0.26	0.78	0.81	0.81	1
	ΔA	2	0.73	0.52	0.93	0.51	0.71
Drought	$\Delta\Psi_{PD}$	2	34.48	< 0.001	0.18	-	-
	Δg_s	2	100.4	< 0.001	0.96	-	-
	ΔA	2	189.4	< 0.001	1	-	-

Cynophalla flexuosa

Treatment	ANOVA				Tukey HSD		
					Time		
	Source	df	F value	P value	(5-0)x(10-0)	(5-0)x(15-0)	(10-0)x(15-0)
Control	$\Delta\Psi_{PD}$	2	2.08	0.21	0.2	0.88	0.37
	Δg_s	2	0.18	0.84	0.99	0.84	0.9
	ΔA	2	0.05	0.95	1	0.96	0.96
Dew	$\Delta\Psi_{PD}$	2	0.19	0.83	0.91	0.83	0.98
	Δg_s	2	4.91	0.06	0.08	0.08	1
	ΔA	2	5.11	0.05	0.09	0.06	0.96
Drought	$\Delta\Psi_{PD}$	2	16.86	< 0.05	0.24	< 0.05	< 0.05
	Δg_s	2	0.15	0.87	0.99	0.86	0.93
	ΔA	2	0.03	0.97	0.99	0.97	1

Mimosa caesalpiniifolia

(a) — 20 μm

(b) — 5 μm

(c) — St, Xy, Fl — 100 μm

(d) AdE, Pp, Sp, AbE — 50 μm

(e) Ct — 60 μm

(f) Mc, Mc — 60 μm

Libidibia ferrea

(g) — 50 μm

(h) — 5 μm

(i) St, Fl, Xy, Fb — 100 μm

(j) Pp, Sp — 60 μm

(k) Ct — 50 μm

(l) AdE, St, AbE — 50 μm

Cynophalla flexuosa

(m) — 100 μm

(n) — 10 μm

(o) Fb, Xy, Fl — 100 μm

(p) Pp, Sp, St, St — 100 μm

(q) Ct — 50 μm

(r) AdE, AbE — 100 μm

Mimosa caesalpiniifolia

(a) AdE, Pp, Sp, AbE — 100 μm

(b) AdE, Xy, Pp, Sp — 100 μm

Combretum leprosum

(c) Tr, AdE, Pp, Sp, Tr — 100 μm

(d) Tr, Pp, Pm, Sp, Tr — 100 μm

Libidibia ferrea

(e) AdE, Pp, Xy, Sp, Fb, AbE — 100 μm

(f) Xy, AdE — 100 μm

Cynophalla flexuosa

(g) AdCt, AdE, Pp, Sp, AbCt, AbE — 100 μm

(h) AdCt, Pp, Xy, Sp, AbCt — 100 μm

(a) *Mimosa caesalpiinifolia*
$R^2=0.38$
$P<0.02$
Hydroscape

(b) *Combretum leprosum*
$R^2=0.34$
$P<0.001$
Hydroscape

(c) *Libidibia ferrea*
$R^2=0.96$
$P<0.0001$
Hydroscape

(d) *Cynophalla flexuosa*
$R^2=0.99$
$P<0.0001$
Hydroscape

Ψ_{min} (MPa)

Ψ_{soil} (MPa)