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Original article

Is leaf water repellency related to vapor pressure deficit and crown exposure in tropical forests?

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ABSTRACT

Environmental conditions can have major influences in shaping biophysical properties of leaf surfaces. In moist environments, high leaf water repellency (LWR) is expected because the presence of a water film on leaf surfaces can block stomatal pores, reduce the diffusion of CO_2, promote pathogen incidence, colonization of epiphylls and leaching of leaf nutrients. However, LWR can also increase in dry environments as a consequence of higher epicuticular wax deposition induced by high temperatures, high radiation loads and vapor pressure deficits (VPD), which could also lead to a high leaf mass per area (LMA). The aim of this study was to determine how LWR varies among tropical trees with contrasting crown exposures and subjected to distinct vapor pressure deficits at different altitudes in the Atlantic Rain Forest. We hypothesized that (i) LWR will be higher in overstory species because they are more frequently exposed to higher radiation and higher vapor pressure deficit; (ii) In the Montane Forest, LWR will be higher for overstory species in comparison to those in Lowland Forest because radiation and VPD increase with altitude; (iii) Overstory species will also show higher LMA in response to exposure to drier conditions. We measured LWR by observing angles of droplets on adaxial and abaxial leaf surfaces in five species co-occurring at lowland and a montane forest. LWR was positively related to crown exposure and VPD at both sites but not to LMA. LWR was significantly higher in the Montane forest (mean angle 66.25°) than in the Lowland forest (mean angle 61.33°). We suggest that atmospheric conditions associated with contrasting crown exposures may exert important controls over leaf surface properties involved in the repellence or direct absorption of water.

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1. Introduction

Leaf water repellency (LWR) is an important functional trait influencing plant performance in distinct habitats (Neinhuis and Barthlott, 1997; Holder, 2007a, 2007b). Different leaf structures that affect leaf surface roughness such as trichomes (Brewer et al., 1991), wax crystals, cuticular folds and epicuticular wax (Neinhuis and Barthlott, 1997) are responsible for variation in LWR. Since water can block stomatal pores and reduce the diffusion of CO_2 (Nobel, 1999), highly repellent leaf surfaces that minimize water bead formation on leaves can be beneficial by allowing gas exchange even under wet conditions (Smith and McClean, 1989; Ishibashi and Terashima, 1995; Shirtcliffe et al., 2006). Other benefits conferred by high LWR in moist environments include reductions in pathogen incidence (Reynolds et al., 1989), colonization of epiphylls (Holder, 2007a), pollutant deposition (Cape, 1996) and leaching of leaf nutrients (De Luca D'oro and Trippi, 1987). At the ecosystem level, high LWR can affect the water balance by increasing the water input through stemflow, fog precipitation and throughfall (Holder, 2007b). In addition to LWR, other leaf traits such as leaf angle (Holder, 2007a) and leaf shape (drip-tips) (Panditharathna et al., 2008) can promote water shedding from leaf surfaces in wet environments.

Dry conditions, especially in open habitats, can also select for leaves with high LWR (Holder, 2007a, 2007b). Epicuticular wax deposition increases on leaves under high temperatures, radiation loads, vapor pressure deficits and water deficits, as a mechanism to minimize water losses and overheating by increasing reflectance (Meinzer, 1982; Sánchez et al., 2001; Mohammadian et al., 2007). In addition, wax layers and other structures such as trichomes, thick cell walls, fibers, sclereids and thick cuticles have been associated with a high leaf mass per area (LMA) in species occurring in

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nutrient and/or water-limited environments (Witkowski and Lamont, 1991; Baldini et al., 1997; Niinemets, 2001). For plants occurring under stressful conditions, high LMA has been reported as a common trait that improves nutrient and water use efficiency (Loveless, 1961; Chabot and Hicks, 1982; Niinemets, 2001), protection from solar radiation (Jordan et al., 2005) and protection against herbivory (Turner, 1994).

Increases in radiation, temperature and vapor pressure deficit along altitudinal gradients (Körner, 2007) can induce modifications in leaf morphological traits (Grubb, 1977; Velázquez-Rosas et al., 2002). In a broad comparison among tropical forests under contrasting climates, Holder (2007a, 2007b) showed that leaves in dry tropical forest tend to have higher LWR values than at Montane sites. In addition, variation in leaf traits in dry and moist forests seems to be related to crown exposure (CE) reflecting the way species cope with distinct abiotic factors (Poorter, 2009). Thus, LWR affects plant responses by (i) increasing water use efficiency (Smith and McClean, 1989; Pandey and Nagar, 2002), (ii) minimizing risks of ice formation on leaves (Aryal and Neuner, 2010) and (iii) promoting water input in soils of dry sites (Holder, 2007a). Therefore, many authors consider LWR as a functional trait that might promote an increase in plant performance in dry and open habitats (Pandey and Nagar, 2002; Holder, 2007a), and along altitudinal gradients from tropical to alpine zones (Aryal and Neuner, 2010).

Along the Brazilian coast, the Atlantic Rain Forest is an ideal ecosystem to test hypotheses about environmental influences on LWR because it provides gradients of abiotic factors associated with forest structure and altitudinal variations. Here, we addressed the following questions: will species that co-occur at different altitudes and with different crown exposures (CE) show different LWR? Taking into account the vertical gradient of abiotic factors, does LWR vary according to the CE of the species within the forest? What is the relationship between LMA and LWR? We hypothesized that (i) Despite the lower evaporative demand in shaded environments, LWR will be greater in overstory species because they are more frequently exposed to direct radiation and higher vapor pressure deficit; (ii) At the Montane Forest, LWR will be greater for overstory species in comparison to those in Lowland Forest because total radiation and VPD increases with altitude; (iii) As well as high LWR, overstory species will show higher LMA in response to drier conditions.

2. Material and methods

2.1. Study site and species

Our study was conducted in lowland and montane forests in the Serra do Mar State Park, which is the largest protected area of Atlantic Rain Forest and covers 315,000 ha in the north of São Paulo state, Brazil. The Lowland forest is 100 m above sea level (23°31′–23°34′S and 45°02′–45°05′W) and has a tropical climate without a marked dry season and a mean annual precipitation of 2200 mm. Usually, the driest months are July and August. The Montane forest is 1000 m above sea level (23°17′–23°24′S and 45°03′–45°11′W) and has a tropical temperate climate. Mean annual precipitation is approximately 2000 mm and frequent fog events occur in comparison to the Lowland forest. All physiognomies are characterized as broadleaf evergreen forests.

We classified the crown exposure (CE) of trees according to Clark and Clark (1992), where the crowns are classified according to an illumination index from 1 (when the tree does not receive any direct light) to 5 (emergent crown, fully exposed) (Table 1). The species were selected according to the following criteria: co-occurrence at both sites, species with different canopy position (overstory, intermediary and understory) and species belonging to different families to avoid phylogenetic effects. We studied five species co-occurring at the Lowland and at the Montane Forest at the Atlantic Rain Forest to assess whether species with contrasting crown exposures would show distinct LWR. The following species were chosen: *Hyeronima alchorneoides* Allemão (Phyllantaceae), *Alchornea triplinervea* (Spreng.) Müll. Arg. (Euphorbiaceae), *Mollinedia schottiana* (Spreng.) Perkins (Monimiaceae); *Euterpe edulis* Mart. (Arecaceae) and *Rustia formosa* Klotzch (Rubiaceae). For simplicity, we will refer to each species by their generic names.

2.2. Leaf water repellency and leaf mass per area

In February 2009, seventy leaves for each species, from ten individuals per species, were collected for leaf water repellency measurements, which were made on the abaxial and adaxial leaf surfaces for each species and estimated as the contact angle (θ) between a water droplet and the leaf surface (Holder, 2007a). After the leaf surface was dried with an absorbent filter paper, the leaf was pinned onto a styrofoam platform to flatten the leaf surface and expose the leaf's horizontal profile. A 10-μl droplet of distilled water was placed onto the leaf surface using a Micropipette (P100, Pipetman, Gilson SAS, Villiers-le-Bel, France) to represent a raindrop as described by Holder (2007a). A photograph of a profile of the water droplet resting on the leaf surface was taken with a digital camera Nikon Cool Pix P80 (135MM F/2.8–4.5 AF − 10 Megapixel; Nikon Corporation, Tokyo, Japan). From the digital image, the θ of the leaf surface and the line tangent to the droplet through the point of contact was measured using the free software ImageJ, version 1.37, (National Institutes of Health, USA, http://www.rsd.info.nih.gov/ij/). The θ was measured relative to the horizontal

Table 1
The mean and standard error (SE) of leaf water repellency (in degrees) of adaxial and abaxial surfaces, leaf mass per area (LMA) for each species within each site and crown exposure (CE). Adaxial and abaxial leaf surfaces were significantly different at $P < 0.05$(*); $P < 0.01$ (**); $P < 0.001$ (***) based on t test. Bold numbers indicate on which leaf surface the leaf water repellency was higher. Different letters indicate significant differences among species within each site (ANOVA, $P < 0.05$).

Site	Species	LWR Adaxial		LWR Abaxial		LMA (g m^{-2})		Crown Exposure	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Lowland Forest	Alchornea***	62.17	1.54	**68.61**	1.35	75.27 ab	12.04	4.5	0.19
	Euterpe*	**51.21**	1.76	44.68	1.21	80.11 ab	7.7	3.01	0.30
	Hyeronima**	69.83	2.38	**77.92**	2.66	82.38 b	6.24	5.0	0
	Mollinedia	47.22	2.34	50.03	1.71	48.09 a	4.47	3.04	0.07
	Rustia ***	**64.73**	2.35	50.1	0.36	58.35 ab	7.06	4.0	0.25
Montane Forest	Alchornea*	63.88	2.27	**69.88**	2.36	86.62 a	4.91	4.96	0.04
	Euterpe**	**61.27**	1.9	51.47	1.71	88.16 a	16.07	3.0	0.20
	Hyeronima	74.95	2.55	70.47	2.04	78.17 a	3.44	4.94	0.04
	Mollinedia	59.19	2.05	60.74	2.26	61.33 a	6.11	3.0	0.15
	Rustia	65.89	2.79	63.57	1.8	73.83 a	3.96	4.0	0.28

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leaf surface. Based on previous studies, leaves surfaces are classified as super-hydrophilic ($\theta < 40°$), highly wettable ($40° < \theta < 90°$), wettable ($90° < \theta < 110°$), non-wettable ($110° < \theta < 130°$), highly non-wettable ($130° < \theta < 150°$) and super-hydrophobic ($\theta > 150°$) (Smith and McClean, 1989; Aryal and Neuner, 2010).

All leaves were digitized (100 dpi) to estimate leaf area and leaf circularity using ImageJ, version 1.37, (National Institutes of Health, USA, http://www.rsd.info.nih.gov/ij/). Leaves were then oven-dried for at least 48 h at 70 °C and weighed. From these data the LMA (g m^{-2}) was calculated as leaf mass per unit leaf blade area.

2.3. Micrometeorological variables

At each altitude three temperature and relative humidity sensors (HOBO, Onset Computer Corporation), set to gather data every 30 min, were placed at different heights at approximately 20 m (canopy), 10 m (intermediary) and 2 m (understory) from the ground at both sites. These data were used to calculate atmospheric vapor pressure deficit (VPD). Mean values for each height and site were calculated from a temporal series of three hundred days. We considered zero VPD data, in non-rainfall periods, as a proxy to estimate the number of days with fog events in each site. Global solar radiation (MJ m^{-2}) data in both sites were obtained from global solar radiation sensors (MODEL 200SA Pyranometer, Microcom Design Inc, Hunt Valley, MD, USA). At the Lowland forest, the sensor was placed at 2 m height in a site clearly unobstructed for daylight conditions. At the Montane forest, it was necessary to place the sensor above the canopy, at 35 m height, for unobstructed daylight conditions. The global solar radiation data were also available as a dataset provided by the Centro de Previsão de Tempo e Estudos Climáticos (CPTEC/INPE) website (http://www.cptec.inpe.br/). The mean values correspond to a one year period of daily integral of radiation energy that we used to calculate monthly averages.

2.4. Statistical analysis

Linear regressions were performed between LWR on both leaf faces and mean VPD, CE and LMA. Tests of significance of differences between means were performed for each species within study sites to determine differences between the LWR of adaxial and abaxial surfaces. Nested ANOVA was used to test whether there were significant differences in LWR in the five species and between the two sites. Species were nested within study sites, leaves were nested within species and leaf surfaces were nested within leaves (Holder, 2007a, 2007b). When analysis of variance showed significant differences among species, we used Tukey HSD multiple comparison tests to determine which pairs of species and leaf faces exhibited significant differences (Holder, 2007a, 2007b). We used paired *t*-tests to compare VPD and solar radiation between sites. All data analysis were done using the R software, version 2.11.1, 2010, http://www.R-project.org.

3. Results

Global solar radiation was significantly higher in the Montane (12.0 MJ m^{-2}) in comparison to the Lowland forest (8.6 MJ m^{-2}) throughout the year (paired t test $= -4.60$; df $= 13$; $P < 0.0001$). Mean VPD was also higher in the Montane forest (0.21 kPa) than in the Lowland forest (0.15 kPa; paired t test $= -5.72$; df $= 13$; $P < 0.0001$) and increased from the understory to the overstory in both sites (Fig. 1). Irrespective of day or night, the stratification of VPD in the canopy profile did not change along the seasons (data not shown). Using zero VPD data, we found that fog occurred during 100 days in the Montane Forest and 34 days per year at the Lowland Forest. Fog duration was also higher at the Montane Forest, as zero VPD data represented 26.4% of the whole VPD dataset (registered every 30 min) at this site and 4.4% at the Lowland Forest during a year.

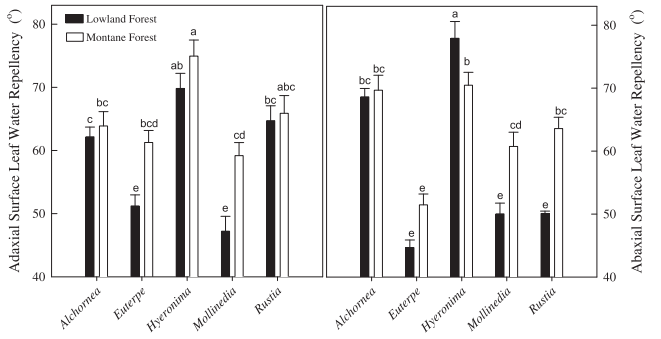

Fig. 1. Comparison of leaf water repellencies between Lowland and Montane Forest for each leaf surface. Different letters indicate significant differences among species for each leaf surface (Tukey HSD multiple pairwise comparison, $P < 0.05$).

We found differences in LWR between sites, species, leaves and leaf faces (Table 2). LWR showed significant differences between species and between adaxial and abaxial leaf surfaces (Table 2, Fig. 1). Leaf water repellency was significantly higher at the Montane forest (mean angle 66.25°) than Lowland forest (mean angle 61.33°; Table 2). In the Lowland Forest, *Euterpe* and *Rustia* showed higher LWR of the adaxial surfaces while *Alchornea* and *Hyeronima* had higher abaxial LWR (Table 1, Fig. 1). In the Montane Forest only *Euterpe* and *Alchornea* showed differences between leaf surfaces as also observed in the Lowland site. At both altitudes, LWR did not show a clear trend of differences between leaf faces (Table 1).

Within species, LWR of each leaf surface did not vary for canopy species between altitudes in most cases (Fig. 1). However, *Euterpe*, *Mollinedia* and *Rustia* had significant lower LWR in the Lowland Forest especially on the abaxial surfaces (Fig. 1). In general, the overstory species had higher LWR on both leaf faces and at both altitudes (Fig. 1). LWR of the adaxial surface was positively related to CE ($R^2 = 0.89$, $P < 0.05$) and VPD ($R^2 = 0.87$, $P < 0.05$) only in the Lowland Forest (Fig. 2). For the abaxial surface, LWR was positively associated with CE in Lowland ($R^2 = 0.84$, $P < 0.05$) and with CE and VPD in Montane Forest ($R^2 = 0.82$, $P < 0.05$; $R^2 = 0.77$, $P < 0.05$, respectively; Fig. 2). For our study sites, the vertical stratification of daytime and nighttime VPD were similar, therefore the relationships between daylight and nighttime VPD with LWR were not different. The LMA variation among species was 1.41-fold for the Lowland site and 1.44-fold for the Montane site. In the Lowland site LMA was highest in *Hyeronima* while *Mollinedia* had the lowest values (Table 1). Despite the lack of significant differences among species in the Montane site, *Rustia* and *Mollinedia*, showed a trend of increase of LMA from the Lowland to the Montane forest. For both leaf faces in both sites, the relationship between LWR and LMA was not significant.

Table 2
Summary of results of the Nested ANOVA for each level.

	df	SS	MS	*F*
Site	1	5077	5076.9	1880.88***
Site : Species	8	52417	6552.1	2427.4***
Site : Species : Leaf	690	90491	235.7	87.304*
Site : Species : Leaf : Leaf Face	700	24113	61.5	22.789*

*$P < 0.05$; ***$P < 0.0001$.

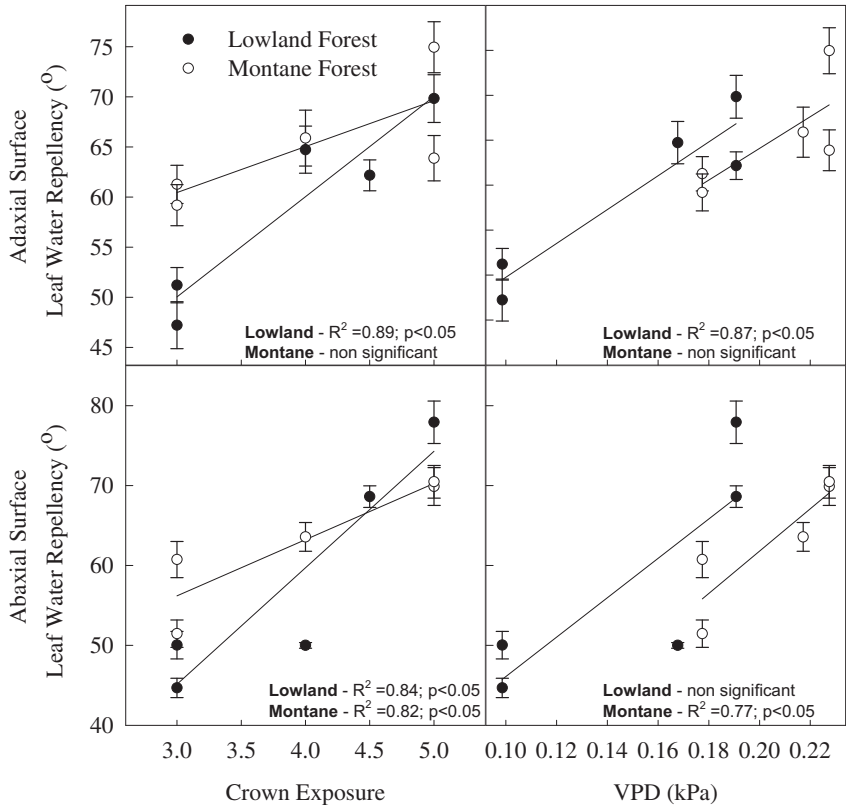

Fig. 2. Relationships between adaxial surface LWR, crown exposure and VPD in the Lowland ($y = 19.50 + 10.11x$ and $y = 30.98 + 187.89x$, respectively) and Montane forest (non-significant relationships) and between abaxial surface LWR, crown exposure and VPD in the Lowland ($y = 0.23 + 14.84x$, non-significant, respectively) and Montane forest ($y = 34.51 + 7.21x$, $y = 8.89 + 264.51x$, respectively).

4. Discussion

Leaf trait variation from understory to canopy and along altitudinal gradients have been consistently described in the literature (Williams et al., 1989; Witkowski and Lamont, 1991; Niinemets, 2001; Panditharathna et al., 2008; Beaumont and Burn, 2009; Aryal and Neuner, 2010). Our findings are similar to those observed by Aryal and Neuner (2010) where LWR increases along an altitudinal gradient and decreases from the canopy to the understory. However, while our study was performed at tropical forests located at 100 and 1000 m above the sea level, their study comprised a different range of elevation (from 186 to 5268 m above sea level) and ecosystems (from tropical to alpine climatic zones) in the Central Himalayas, Nepal. In their study, the functional meaning of higher LWR, considered as highly non-wettable ($130° < \theta < 150°$), was preferentially related to avoidance of ice formation that could cause damage to leaf tissues in plants frequently exposed to freezing temperatures. In contrast, our LWR data (from 44.68° to 77.92°) are within the range of highly wettable leaves as observed for other tropical environments (Holder, 2007a; Aryal and Neuner, 2010). Despite the small range of variation of LWR in our study sites, we showed that CE and VPD were positively related to LWR, suggesting that exposition to drier conditions might stimulate epicuticular wax exudation from epidermic and guard cells (Meinzer, 1982; Sánchez et al., 2001; Mohammadian et al., 2007). Thus, even subtle increases in LWR through wax deposition could minimize sharp declines in leaf water potential, strong stomatal closure and decreases in photosynthesis (Myers et al., 1987; Santiago et al., 2000; Jordan et al., 2005; Motzer et al., 2005).

We found that LWR was also higher for overstory species. Similarly, wetness on leaf surfaces decreases from understory to canopy in montane tropical forests in Colombia as a consequence of low relative humidity and high radiation in the canopy (Letts and Mulligan, 2005). In that study, Letts and Mulligan (2005) found that at 10 m height, mean wetness on leaf surfaces is around 14%, suggesting that water beads do not form very frequently on exposed leaves. This finding reinforces the view that high LWR might be related to factors different from those exclusively related to avoidance of leaf wetting on exposed leaves. Additionally, higher LWR has been reported for drier sites (Holder, 2007a, 2007b) and in plants occurring in more open habitats (Pandey and Nagar, 2002; Aryal and Neuner, 2010) where leaf wetting is less common. In contrast to studies where changes in leaf structures in response to environmental conditions (Meinzer, 1982; Baldini et al., 1997; Sánchez et al., 2001; Jordan et al., 2005; Mohammadian et al., 2007) lead to alterations in LWR (Neinhuis and Barthlott, 1997), we did not find any relationship between LMA and LWR. LMA is the product of different structures such as thick cell walls, fibers and sclereids (Witkowski and Lamont, 1991; Baldini et al., 1997; Niinemets, 2001), which may not affect the biophysical characteristics of leaf surfaces, and therefore LWR.

There is increasing evidence to show that when a leaf gets wet, water might be either repelled or directly absorbed (Burgess and Dawson, 2004; Oliveira et al., 2005; Zimmermann et al., 2007; Simonin et al., 2009). Leaf water uptake (LWU) seems to be a common mechanism among terrestrial plants that might contribute positively to the maintenance of key physiological processes. Plants that are able to absorb water via leaves during periods of soil water deficit may increase their leaf water content, leaf water potential, stomatal conductance and rates of gas exchange (Burgess and Dawson, 2004; Simonin et al., 2009; Burkhardt, 2010). In addition, Simonin et al. (2009) suggested

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that the negative effect of low LWR would be short lived, since the positive physiological effects (e.g. increased rates of gas exchange) take place after leaf surfaces have dried. However, the benefits associated with high LWU capacity will depend on the frequency of events promoting leaf wettability and soil water availability.

In conclusion, we showed that LWR varied according to crown exposure and VPD at both sites, supporting the well-observed trends of leaf trait variation along environmental gradients. However, it is important to highlight the role of CE to changes in LWR. Our results suggest that the functional significance of LWR is related to different CE and to different atmospheric conditions which plants are subjected to. Thus, further studies considering leaf trait variation along altitudinal gradients should consider differences associated with strata position and crown exposure. Additionally, much larger datasets are necessary to elucidate the tradeoffs between the repellent versus absorptive abilities of leaf surfaces and their interplay with other leaf traits and atmospheric conditions.

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