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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.

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