

PATTERNS OF LEAF WETTABILITY ALONG AN EXTREME MOISTURE GRADIENT IN WESTERN PATAGONIA, ARGENTINA

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The objective of this study was to investigate patterns of surface features of leaves related to susceptibility to wetness for plants along a strong precipitation gradient. Leaf wettability and droplet retention were examined for leaves of 37 species (representing 28 families) occurring in steppe, ecotone, and temperate rain forest habitats along a steep moisture gradient in northwestern Patagonia, Argentina. Morphological and structural characteristics of leaves significantly affected leaf surface wetness, and these characteristics varied between habitats. Typically, leaves had more stomata on abaxial than adaxial leaf surfaces ($P < 0.0001$). Droplet retention and leaf wettability (θ) were negatively correlated (Spearman $r = -0.694$; $P < 0.0001$). Leaves in dry habitats tended to be less wettable and less likely to retain droplets on the leaf surface; however, overall differences were not significant. The presence of trichomes significantly reduced wettability ($P < 0.05$). The high frequency and natural variability of wetting events in these and a great variety of other habitats, coupled with the large range in surface wettability among plant species and the potentially strong effects on photosynthesis, growth, and pathogen infections, suggest an important evolutionary avenue related to the dynamics of water on leaf surfaces.

Keywords: leaf wetness, morphology, water droplet, Patagonia, gradient.

Introduction

A large variety of terrestrial plants experience periods of leaf wetness during some part of the growing season as a result of rain, ground fog, and cloud mist. The extent and duration of leaf surface wetness has physiological, ecological, and anthropogenic importance. For example, the importance to possible pathogen invasion is especially well documented for agricultural and native species (Butler 1996; Bradley et al. 2003). Concerns for pollutant deposition and nutrient leaching in both native and agricultural plants have stimulated many studies on leaf wetness from dew as well as rainfall (Tukey 1970; Massman et al. 1994; Schreuder et al. 2001).

Many studies have documented important structural differences among the leaf surfaces of many plant species, which strongly influence the extent and duration of leaf surface wetness (Lightbody 1985; Brewer et al. 1991; Brewer and Smith 1997; Neinhuis and Barthlott 1997). Previous studies considered factors such as leaf surface repellency (i.e., the tendency to form droplets vs. water films; Martin and Juniper 1970; Brewer et al. 1991), the influence of trichomes (Challen 1962; Brewer et al. 1991; Brewer and Smith 1997; Panday and Nagar 2003), leaf orientation (Bradley et al. 2003), and the presence of leaf surface irregularities (Challen 1960; Neinhuis and Barthlott 1997). Furthermore, some groups of plants appear to avoid deposition of dewfall by being thermally coupled to a warm substrate (Brewer and Smith 1995).

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Studies relating leaf surface wetness to growth have focused on nutrient uptake and the possible absorption of atmospheric water in both mesic and xeric environments (Mooney et al. 1980; Schmitt et al. 1989; Yates and Hutley 1995; Martin and von Willert 2000; Burgess and Dawson 2004), as well as potential reductions in transpirational water loss (Stone 1963) and CO₂ uptake (Benzing and Renfrow 1971; Brewer and Smith 1994, 1995; Ishibashi and Terashima 1995; Rice and Giles 1996). In humid tropical systems, where the leaf surfaces of many plants may remain wet for most or all of the day, some investigators have suggested the potential for plant nutrient limitations due to low transpiration rates and, thus, reduced nutrient uptake from the soil (Weaver et al. 1973; Ash 1987), though this hypothesis has not been widely supported (Bruijnzeel and Veneklaas 1998; Tanner et al. 1998). Leaf wetness also has been shown to affect photosynthetic gas exchange and growth via influences on stomata and CO₂ uptake (Brewer and Smith 1994; Ishibashi and Terashima 1995; Rice and Giles 1996; Field et al. 1998; Hanba et al. 2004; Letts and Mulligan 2005) and predicted slow diffusion of CO₂ through films of water compared with air.

Given the many ecological and physiological consequences of pooled water on leaf surfaces, the objective of this study was to investigate patterns of surface features of leaves and relate them to leaf surface wettability for plants in different habitats along a steep rainfall gradient. We predicted that plants in habitats most susceptible to leaf wetting (i.e., greater precipitation) would have lower droplet retention and greater contact angles, resulting in shorter durations of wet surfaces, than plants in habitats that rarely experienced periods of leaf wetting. An ideal location to evaluate patterns of leaf wetness is northwestern Patagonia in Argentina

Table 1
Species Collected in the Vicinity of San Carlos de Bariloche, Argentina

Family/species	Habit	Habitat	Precipitation (mm)	Trichome		θ		Retention	
				AD	AB	AD	AB	AD	AB
Alstroemeraceae:									
<i>Alstroemeria aurea</i> Graham	Herb	Ecotone	1100	–	–	163.5 (1.3)	150.5 (6.3)	4.2 (1.8)	33 (5.1)
Anacardiaceae:									
<i>Schinus patagonicus</i> (Phil.) I.M. Johnst.	Tree	Ecotone	1300	–	–	82.5 (7.6)	76.5 (4.6)	89.8 (.2)	89.0 (1.0)
Apiaceae:									
<i>Osmorhiza chilensis</i> Hook & Arn.	Herb	Ecotone	1300	+	+	96.8 (15.2)	99.5 (2.6)	86.0 (4.0)	66.4 (6.4)
Araliaceae:									
<i>Pseudopanax laetevirens</i> (Gay) Franch	Tree	Rain forest	3000	–	–	36.8 (5.2)	69.0 (4.4)	57.6 (2.7)	83.2 (4.7)
Asteraceae:									
<i>Bacchans magellanica</i> (Lam.) Pers.	Cushion	Steppe	750	–	–	90.0 (.0)	90.0 (.0)	90.0 (.0)	90.0 (.0)
<i>Dasyphyllum diacanthoides</i> (Less.) Cabrera	Tree	Rain forest	3000	+	+	44.8 (3.0)	56.3 (4.9)	71.4 (7.2)	60.8 (4.8)
Atherospermataceae:									
<i>Laureliopsis philippiana</i> (Looser) Schodde	Tree	Rain forest	3000	–	+	25.8 (4.8)	45.5 (5.3)	51.4 (2.6)	90.0 (.0)
Berberidaceae:									
<i>Berberis buxifolia</i> Lam.	Shrub	Ecotone	1300	–	+	120.8 (6.3)	133.5 (3.6)	34.2 (5.9)	7.2 (4.4)
<i>Berberis darwinii</i> Hook.	Shrub	Rain forest	3000	–	–	43.3 (5.4)	64.0 (5.0)	49.2 (4.9)	90.0 (.0)
Bignoniaceae:									
<i>Campsidium valdivianum</i> (Phil.) Skottsb.	Liana	Rain forest	3000	–	–	44.0 (6.2)	70.8 (3.8)	45.6 (4.4)	66.6 (8.3)
Calyceraceae:									
<i>Boopis anthemoides</i> Juss.	Cushion	Steppe	750	–	–	90.0 (.0)	130.0 (.0)	90.0 (.0)	54.0 (22.0)
Celastraceae:									
<i>Maytenus boaria</i> Mol.	Tree	Ecotone	1300	–	–	60.5 (7.1)	77.5 (1.0)	88.8 (1.2)	79.4 (4.0)
Cunoniaceae:									
<i>Weinmannia trichosperma</i> Cav.	Tree	Rain forest	3000	–	–	37.5 (7.6)	75.8 (1.7)	42.2 (2.2)	80.0 (4.9)
Desfontaineaceae:									
<i>Desfontainea spinosa</i> Ruiz et Pavón	Shrub	Rain forest	3000	–	+	66.8 (5.6)	64.5 (4.9)	90.0 (.0)	90.0 (.0)
Eleocarpaceae:									
<i>Aristotelia chilensis</i> (Mol.) Stuntz	Tree	Ecotone	1800	–	–	38 (3.5)	49.5 (3.4)	90.0 (.0)	84.8 (3.8)
Ericaceae:									
<i>Gaultheria phillyreifolia</i> (Pers.) Sleumer	Shrub	Rain forest	3000	–	–	52.8 (5.3)	62.3 (3.8)	47.6 (2.1)	78.0 (5.5)
<i>Gaultheria mucronata</i> (L.F.) Hook. & Arn	Shrub	Ecotone	1300	–	–	62.5 (5.4)	83.0 (4.8)	57.2 (7.2)	84.0 (3.3)
Fabaceae:									
<i>Vicia nigricans</i> Hook. et Arn.	Herb	Woodland	1300	+	+	180 (.0)	85.3 (10.0)	.0 (.0)	73.2 (7.3)
Fagaceae (Nothofagaceae):									
<i>Nothofagus dombeyi</i> (Mirb.) Oesrt.	Tree	Ecotone	1200	–	–	50.0 (2.5)	60.8 (5.0)	90.0 (.0)	77.8 (7.5)
Flacouritaceae:									
<i>Azara lanceolata</i> Hook f.	Shrub	Rain forest	3000	–	+	22.0 (1.8)	38.0 (2.8)	63.6 (3.7)	76.0 (6.6)
Hydrangeaceae:									
<i>Hydrangea serratifolia</i> (Hook. et Arn.) F. Phil.	Liana	Rain forest	3000	–	–	42.8 (2.8)	57.3 (4.9)	64.0 (4.0)	62.0 (2.1)
Loranthaceae:									
<i>Tristerix corymbosus</i> (L.) Kuijt	Hemiparasite	Ecotone	1800	–	–	70.8 (8.3)	71.5 (4.3)	90.0 (.0)	90.0 (.0)

Table 1
(Continued)

Family/species	Habit	Habitat	Precipitation (mm)	Trichome		θ		Retention	
				AD	AB	AD	AB	AD	AB
Myrtaceae:									
<i>Luma apiculata</i> (D.C.) Burret	Tree	Rain forest	3000	–	+	62.5 (1.3)	17.5 (12.5)	62.0 (10.4)	69.2 (5.6)
Oxalidaceae:									
<i>Oxalis adenophylla</i> Gilles ex Hook. et Arn.	Cushion	Steppe	750	–	–	160.0 (.0)	160.0 (.0)	20.0 (.0)	20.0 (.0)
Poaceae:									
<i>Chusquea culeou</i> Desv.	Shrub	Rain forest	3000	–	+	32.5 (4.1)	91.8 (16.6)	36.8 (4.0)	50.8 (3.5)
Proteaceae:									
<i>Embothrum cocineum</i> J.R. Forst et G. Forster	Tree	Rain forest	3000	–	–	47.0 (3.9)	51.5 (3.2)	61.2 (4.0)	75.0 (6.7)
<i>Lomatia ferrunginea</i> (Cav.) R. Brown	Tree	Rain forest	3000	+	+	28.5 (3.2)	75.5 (12.1)	48.0 (3.8)	62.2 (9.6)
<i>Lomatia hirsuta</i> (Lam.) Diels ex J.F. Macbr.	Tree	Ecotone	1800	–	–	46.5 (7.6)	44.8 (3.9)	83.2 (3.1)	85.4 (1.9)
Ranunculaceae:									
<i>Anemone multifida</i> Poir.	Herb	Ecotone	1300	+	+	75.3 (8.0)	87.3 (9.2)	70.6 (2.2)	79.0 (5.4)
Rosaceae:									
<i>Acaena ovalifolia</i> Ruiz et Pavón	Herb	Rain forest	3000	–	+	71.3 (7.8)	170.0 (5.8)	90.0 (.0)	.0 (.0)
<i>Acaena pinnatifida</i> Ruiz et Pavón	Cushion	Steppe	750	+	+	160.0 (.0)	180.0 (.0)	22.0 (9.7)	9.0 (5.6)
<i>Acaena splendens</i> Gillies ex Hook. et Arn.	Cushion	Steppe	750	+	+	160.0 (.0)	180.0 (.0)	22.0 (1.1)	.0 (.0)
<i>Frageria chiloensis</i> (L.) Duchesne f.	Herb	Rain forest	3000	+	+	106.5 (1.1)	117.5 (8.8)	71.3 (10.1)	90.0 (.0)
<i>Sanguisorba minor</i> Scopoli	Herb	Steppe	750	+	+	160.0 (.0)	180.0 (.0)	17.8 (5.2)	.0 (.0)
Saxifragaceae:									
<i>Ribes magellanicum</i> Poir.	Shrub	Rain forest	3000	–	+	62.5 (1.0)	76.3 (3.6)	81.4 (2.5)	42.2 (5.3)
Violaceae:									
<i>Viola maculata</i> Cav.	Herb	Rain forest	3000	+	+	44.5 (5.3)	66.5 (9.5)	70.0 (8.4)	89.0 (1.0)
Winteraceae:									
<i>Drimys winteri</i> J.R. Forst et G. Forster	Shrub	Rain forest	3000	–	–	48.8 (3.9)	47.5 (6.2)	63.6 (3.7)	81.6 (3.0)

Note. Growth habit and habitat where species were found. Precipitation data summarized from Barros et al. (1983). Trichomes are present (plus sign) or absent (minus sign). Values for θ and droplet retention angle are means + SE for adaxial (AD) and abaxial (AB) leaf surfaces.

because of an abrupt change in precipitation over a short distance with no change in elevation (Barros et al. 1983).

Material and Methods

Study Sites

Collection sites were chosen to take advantage of an extreme moisture gradient running from the Andes to the steppe in Nahuel Huapi National Park (41°16'S, 71°20'W) in the northern region of western Patagonia in Argentina. A total of 37 species (representing 28 families) were surveyed along a west-to-east transect located at ca. 41°S. Selected habitats were (1) steppe (two sites), characterized by the presence of xeric shrubs and tussock grasses; (2) forest-steppe ecotone (four sites), dominated by shrubs (matorral) species; and (3) temperate (Valdivian) rain forest (two sites; table 1). This environmental gradient reflects the abrupt decrease in precipitation that characterizes the region due to the orographic effect of the Andes on westerly moisture. Along this transect from the continental divide to the east, precipita-

tion declines from >3000 mm yr⁻¹ to ca. 300 mm yr⁻¹ in <100 km without a change in elevation. Precipitation is concentrated during austral fall and winter months (April–September), whereas summer months (December–February) are relatively dry and mild. According to data from *Servicio Meteorológico Nacional*, Bariloche Airport Station, Argentina, mean monthly temperature ranges from ca. 2°C in winter (July) to ca. 14°C in the summer (January; Barros et al. 1983; Paruelo et al. 1998).

Leaf Surface Characteristics and Leaf Wettability

Measurements were made on both adaxial (upper) and abaxial (lower) leaf surfaces, including contact angles (θ ; fig. 1a) of water droplets on the leaf surface (leaf wettability), droplet retention (angular value; fig. 1b), trichome presence, stomatal density (number mm⁻²), guard cell length (μ m), and stomatal pore length (μ m). Measurements were made on five randomly selected, fully expanded healthy leaves per species with five replicates per leaf. The degree of water

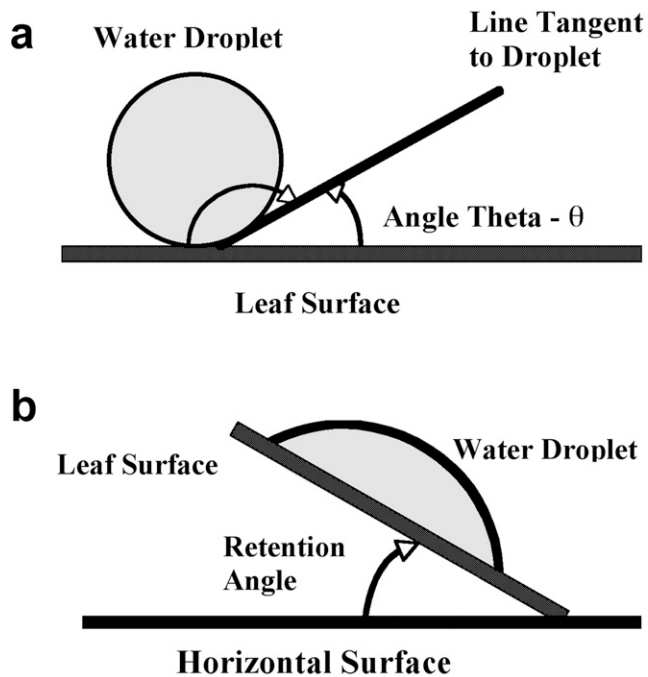


Fig. 1 *a*, Leaf wettability, the angle θ of a line tangent to the point of contact between a droplet and the leaf surface. *b*, Droplet retention, the angle of inclination at which a droplet first begins to roll down the leaf surface.

repellency of the leaf surface was determined by measuring the contact angle of a 5-mm³ water droplet with the leaf surface (Adam 1963). The angle (θ) of a line tangent to the droplet through the point of contact between the droplet and the leaf surface was measured (Brewer et al. 1991; for photo illustration, see Brewer 1996). Leaves with $\theta < 110^\circ$ were considered wettable; those with $\theta > 130^\circ$ were nonwetable (Crisp 1963). For all leaves, θ was measured relative to the epidermis for horizontally positioned leaves, even when droplets rested above the epidermis on trichomes. Given a droplet of a certain volume, θ also provided an index of the amount of the surface of the droplet that is in contact with the leaf and, therefore, the area of leaf surface covered (Brewer et al. 1991).

Droplet retention, an index of the “stickiness” of a leaf surface for water, was measured by placing a 50-mm³ droplet on a leaf surface (initially horizontal) and measuring the angle of leaf inclination at which the droplet first began to move. High angular values ($>60^\circ$) indicate a greater tendency to retain droplets, while low values ($<20^\circ$) indicate leaf surfaces that readily shed droplets.

Stomatal density was estimated from surface impressions (clear enamel nail polish) made from midblade adaxial and abaxial leaf surfaces. Care was taken to avoid veins. The stomatal index was calculated according to Bongers and Popma (1990) as the product of stomatal density and guard cell length. Trichome presence/absence was determined visually using a hand lens ($\times 10$ magnification).

Differences in leaf wettability, droplet retention, and stomatal and trichome density between leaf sides (adaxial or abaxial) and according to habitat type were assessed with a

Kruskal-Wallis one-way ANOVA on ranks using a Tukey test on ranks for pair-wise comparisons (JMP 5.1, SAS Institute). This procedure is robust for unequal sample sizes and slight deviations from normal distributions (Zar 1998). Correlations between variables were assessed with a Spearman correlation procedure. An interesting case was *Alstroemeria aurea* Graham, an herbaceous species with stomata only on the adaxial surface, but with this surface positioned “down” via leaf twisting. Therefore, for our analyses, “functional” sides were considered.

Results

For the 37 species of plants evaluated, there was a broad range in stomatal density, trichome presence, contact angles, and droplet retention angles for adaxial and abaxial leaf surfaces (tables 1, 2). Typical leaves in habitats along this gradient had nearly 30 times more stomata on abaxial than adaxial leaf surfaces ($P < 0.0001$). The incidence of amphistomatous leaves was rare along this gradient, with only three species in each habitat showing this condition (table 2). Most species had stomata only on the abaxial surface. Stomatal density for all species and leaf sides was positively correlated with guard cell length (Spearman $r = 0.52$, $P < 0.0001$), stomatal pore length (Spearman $r = 0.43$, $P < 0.001$), and, therefore, stomatal area index (Spearman $r = 0.88$, $P < 0.0001$).

Comparisons among species showed that the surface with more stomata (typically the abaxial) was less wettable ($P < 0.05$), but there were no significant differences in retention angles when species from all ecosystems were considered. Values for θ in temperate rain forest species were higher on the abaxial compared with adaxial surfaces ($P < 0.01$); however, in other ecosystems, differences for θ were not significant. Overall, there were no differences in retention angles. Droplet retention and θ were negatively correlated (fig. 2; Spearman $r = -0.69$, $P < 0.0001$), and this correlation was stronger when only the abaxial side was considered (Spearman $r = 0.86$, $P < 0.0001$). For all surfaces examined, more spherical droplets ($\theta > 130^\circ$) corresponded to the lowest levels of droplet retention. For glabrous leaves, contact angles were higher (more spherical droplets) on abaxial surfaces (fig. 3a). There was no significant difference in θ for abaxial versus adaxial surfaces in the presence of trichomes (fig. 3a). The presence of trichomes increased the tendency for leaves to form more spherical droplets, resulting in significantly greater contact angles ($P < 0.05$) regardless of surface (fig. 3b). Moreover, there was a trend toward lower retention angles for pubescent versus glabrous leaf surfaces.

The general trend in leaf wettability along the moisture gradients was from high contact angles and spherical droplets for leaf surfaces from the dry steppe to lower contact angles and flattened droplets in the mesic and temperate rain forests (table 3). Species from the steppe tended to have the least wettable surfaces, followed by species in the ecotone, and finally temperate rain forest habitats. Cushion plants, a common type of plant in the steppe, and herbs were less wettable, while trees and lianas tended to be most wettable ($P < 0.001$). Cushions tended to have the greatest incidence of pubescent leaves (table 1).

Table 2

Leaf Surface Characteristics of Species Collected in the Vicinity of San Carlos de Bariloche, Argentina

Family/species	Stomatal density (mm ⁻¹)		Guard cell length (μm)		Stomatal pore length (μm)		Stomatal index (mm ⁻¹)	
	AD	AB	AD	AB	AD	AB	AD	AB
Alstroemeraceae:								
<i>Alstroemeria aurea</i>	51.2 (6.0)	.0 (.0)	64.5 (2.4)	.0 (.0)	41.0 (1.0)	.0 (.0)	3.3 (.5)	.0 (.0)
Anacardiaceae:								
<i>Schinus patagonicus</i>	.0 (.0)	179.2 (6.0)	.0 (.0)	27.0 (1.8)	.0 (.0)	17.5 (1.1)	.0 (.0)	4.8 (.2)
Apiaceae:								
<i>Osmorhiza chilensis</i>	.0 (.0)	105.6 (9.6)	.0 (.0)	25.0 (.8)	.0 (.0)	15.5 (.9)	.0 (.0)	2.6 (.2)
Araliaceae:								
<i>Pseudopanax laetevirens</i>	.0 (.0)	121.6 (8.2)	.0 (.0)	23.5 (1.3)	.0 (.0)	14.0 (1.0)	.0 (.0)	5.0 (.3)
Asteraceae:								
<i>Dasyphyllum diacanthoides</i>	.0 (.0)	121.6 (12.0)	.0 (.0)	34.5 (2.2)	.0 (.0)	19.5 (1.5)	.0 (.0)	2.3 (.3)
Atherospermataceae:								
<i>Laureliopsis philippiana</i>	.0 (.0)	73.6 (10.8)	.0 (.0)	53.5 (1.3)	.0 (.0)	32.5 (2.1)	.0 (.0)	13.1 (.3)
Berberidaceae:								
<i>Berberis buxifolia</i>	.0 (.0)	281.6 (12.0)	.0 (.0)	29.0 (1.0)	.0 (.0)	19.0 (.6)	.0 (.0)	8.2 (.5)
<i>Berberis darwinii</i>	.0 (.0)	368.0 (23.7)	.0 (.0)	28.5 (1.0)	.0 (.0)	16.5 (.6)	.0 (.0)	8.9 (1.0)
Bignoniaceae:								
<i>Campsidium valdivianum</i>	.0 (.0)	243.2 (42.2)	.0 (.0)	26.0 (.6)	.0 (.0)	14.5 (.5)	.0 (.0)	13.1 (2.4)
Celastraceae:								
<i>Maytenus boaria</i>	.0 (.0)	249.6 (13.9)	.0 (.0)	34.5 (.9)	.0 (.0)	18.5 (1.7)	.0 (.0)	8.6 (.4)
Cunoniaceae:								
<i>Weinmannia trichosperma</i>	.0 (.0)	278.4 (27.1)	.0 (.0)	27.0 (1.2)	.0 (.0)	8.0 (.9)	.0 (.0)	7.9 (.7)
Desfontaineaceae:								
<i>Desfontainea spinosa</i>	.0 (.0)	358.4 (21.2)	.0 (.0)	25.5 (2.0)	.0 (.0)	13.5 (1.0)	.0 (.0)	8.7 (.9)
Eleocarpaceae:								
<i>Aristotelia chilensis</i>	.0 (.0)	256.0 (18.2)	.0 (.0)	27.0 (.9)	.0 (.0)	18.5 (1.0)	.0 (.0)	6.9 (.6)
Ericaceae:								
<i>Gaultheria phillyreifolia</i>	.0 (.0)	310.4 (10.9)	.0 (.0)	24.0 (.6)	.0 (.0)	18.0 (.9)	.0 (.0)	4.6 (.3)
<i>Gaultheria mucronata</i>	.0 (.0)	454.4 (26.6)	.0 (.0)	27.5 (.8)	.0 (.0)	16.5 (1.0)	.0 (.0)	12.5 (.9)
Fabaceae:								
<i>Vicia nigricans</i>	57.6 (10.9)	19.2 (3.2)	28.0 (.9)	33.0 (.9)	21.5 (1.3)	24.0 (1.0)	1.6 (.4)	.6 (.1)
Fagaceae (Nothofagaceae):								
<i>Nothofagus dombeyi</i>	.0 (.0)	406.4 (35.6)	.0 (.0)	34.0 (1.3)	.0 (.0)	13.5 (.6)	.0 (.0)	13.8 (1.2)
Flacouritaceae:								
<i>Azara lanceolata</i>	.0 (.0)	435.2 (13.8)	.0 (.0)	24.0 (1.3)	.0 (.0)	16.5 (.6)	.0 (.0)	11.3 (.4)
Hydrangeaceae:								
<i>Hydrangea serratifolia</i>	.0 (.0)	166.4 (18.0)	.0 (.0)	19.0 (1.3)	.0 (.0)	13.5 (1.3)	.0 (.0)	6.3 (.8)
Loranthaceae:								
<i>Tristerix corymbosus</i>	64.0 (11.3)	92.8 (12.8)	30.5 (.9)	41.0 (1.7)	22.6 (1.5)	32.0 (1.7)	2.0 (.4)	2.5 (.3)
Myrtaceae:								
<i>Luma apiculata</i>	.0 (.0)	540.8 (19.2)	.0 (.0)	23.5 (1.7)	.0 (.0)	13.5 (1.0)	.0 (.0)	13.0 (.7)
Poaceae:								
<i>Chusquea culeou</i>	.0 (.0)	92.8 (11.8)	.0 (.0)	20.0 (...)	.0 (.0)	12.5 (...)	.0 (.0)	2.6 (...)
Proteaceae:								
<i>Embothrium cocineum</i>	.0 (.0)	166.4 (8.2)	.0 (.0)	22.5 (1.1)	.0 (.0)	15.5 (1.2)	.0 (.0)	4.2 (.3)
<i>Lomatia ferrunginea</i>	.0 (.0)0 (.0)0 (.0)	17.5 (...)	.0 (.0)	...
<i>Lomatia hirsuta</i>	.0 (.0)	192.0 (13.4)	.0 (.0)	29.0 (.6)	.0 (.0)	15.5 (.5)	.0 (.0)	3.0 (.3)
Ranunculaceae:								
<i>Anemone multifida</i>	38.4 (8.2)	48.0 (5.1)	...	65.0 (2.2)	41.0 (1.4)	46.0 (1.7)	...	3.1 (.3)
Rosaceae:								
<i>Acaena ovalifolia</i>	.0 (.0)	281.6 (37.8)	.0 (.0)	15.0 (.8)	.0 (.0)	18.5 (1.9)	.0 (.0)	7.5 (.8)
<i>Sanguisorba minor</i>	124.8 (15.5)	...	22.0 (.9)	...	15.0 (1.4)	...	2.8 (.4)	...
Saxifragaceae:								
<i>Ribes magellanicum</i>	.0 (.0)	144.0 (16.8)	.0 (.0)	30.5 (.9)	.0 (.0)	19.0 (1.0)	.0 (.0)	5.1 (.9)
Violaceae:								
<i>Viola maculata</i>	.0 (.0)	102.4 (9.6)	.0 (.0)	33.5 (1.3)	.0 (.0)	17.5 (1.4)	.0 (.0)	3.4 (.4)
Winteraceae:								
<i>Drimys winteri</i>	.0 (.0)	86.4 (6.4)	.0 (.0)	37.5 (.8)	.0 (.0)	21.0 (.6)	.0 (.0)	2.0 (.2)

Note. *Boopis anthemoides* (Calyceraceae), *Oxalis adenophylla* (Oxalidaceae), *Acaena splendens*, and *Fragaria chilensis* (both Rosaceae) are not in the table because of difficulty extracting a surface cast from highly pubescent leaves or leaves with stomatal crypts. Stomatal density, guard cell length, stomatal pore length, and stomatal index are means \pm SE for adaxial (AD) and abaxial (AB) leaf surfaces. Ellipses indicate no data.

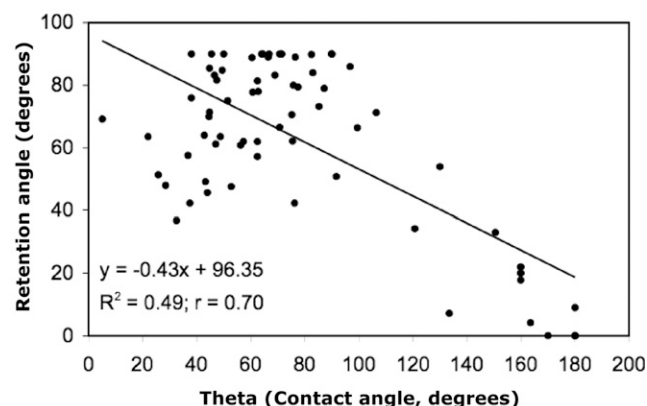


Fig. 2 Droplet retention as a function of the contact angle θ . The model is droplet retention = $-0.439(\theta) + 97.6$ ($R = -0.695$; $P < 0.0001$).

Discussion

The results of this study show that morphological and structural characteristics of leaves significantly affected leaf surface wetness and that these characteristics varied between habitats. In southwestern Argentina, the nature of wetting events during the growing season varies among habitat types along the moisture gradient. Plants in temperate rain forest habitats experienced frequent rainfall, fog, and cloud mist events, which deposited water on leaves. Therefore, plants in these habitats could be wet for days at a time. In contrast, plants in the steppe may have wet leaf surfaces as a result of infrequent summer rain showers and radiational dewfall. Compared with rain forest habitats, the duration of leaf wetness was typically short (minutes to hours only).

In general, leaves that repel water tend to exhibit surprisingly strong surface relief. Neinhuis and Barthlott (1997) attributed surface roughness to trichomes, shapes caused by different cell walls, and characteristics of the type and arrangement of epicuticular waxes. As reported in many previous studies (e.g., Brewer et al. 1991; Brewer and Smith 1994, 1997; Panday and Nagar 2003), the surface with the greatest concentration of stomata was the least wettable, regardless of the habitat type. Lower droplet retention and wettability on the surface with the greatest concentrations of stomata (typically the abaxial surface) is advantageous because they lead to reduced interference of liquid water with photosynthetic gas exchange (Terashima et al. 1993; Brewer and Smith 1994, 1995; Ishibashi and Terashima 1995). Aside from the much slower diffusion of CO_2 through water than air (ca. 10,000 times slower; Weast 1985), large droplets can physically block hundreds of stomata. For example, according to the relationship shown in Brewer et al. (1991), a small droplet on a wettable leaf (e.g., θ of ca. 50°) would cover roughly 0.5 mm^2 but only 0.2 mm^2 on a nonwettable leaf ($\theta > 130^\circ$). Extending these finding to our study, this corresponds to nearly 130 stomata covered on a wettable leaf such as *Aristotelia chilensis* (Mol.) Stuntz but only ca. 50 stomata on a nonwettable leaf such as *Berberis buxifolia* Lam., two species with similar stomatal density (ca. 260 and 280 mm^{-2}) but different wettabilities ($\theta = 49.5$ and 133.5 , re-

spectively). Likewise, accumulation of water on photosynthetic surfaces may precipitate stomatal closure (Ishibashi and Terashima 1995; Hanba et al. 2004). Consequently, either stomatal blockage or closure may cause potentially significant reductions in net photosynthetic gas exchange for wettable compared with nonwettable leaves.

Smaller guard cells have been associated more commonly with plants from xeric habitats compared with mesic habitats. Theory suggests that CO_2 diffusion per area of stomata should be higher with smaller guard cells, resulting in reduced water loss. This should be especially advantageous for plants in dry habitats with high-incident light levels. However, this pattern is not consistently reported in the literature. For example, Abrams and Kubiske (1990) found no consistent pattern between guard cell length and habitat. For species in the habitats along the moisture gradient in Patagonia, there was a trend for the greatest stomatal density and index to be found on plants in the wettest temperate rain forest habitat, whereas the lowest density and index were reported for a species in the xeric steppe. To better evaluate the strength of this trend, more data are needed from species in the most xeric habitats.

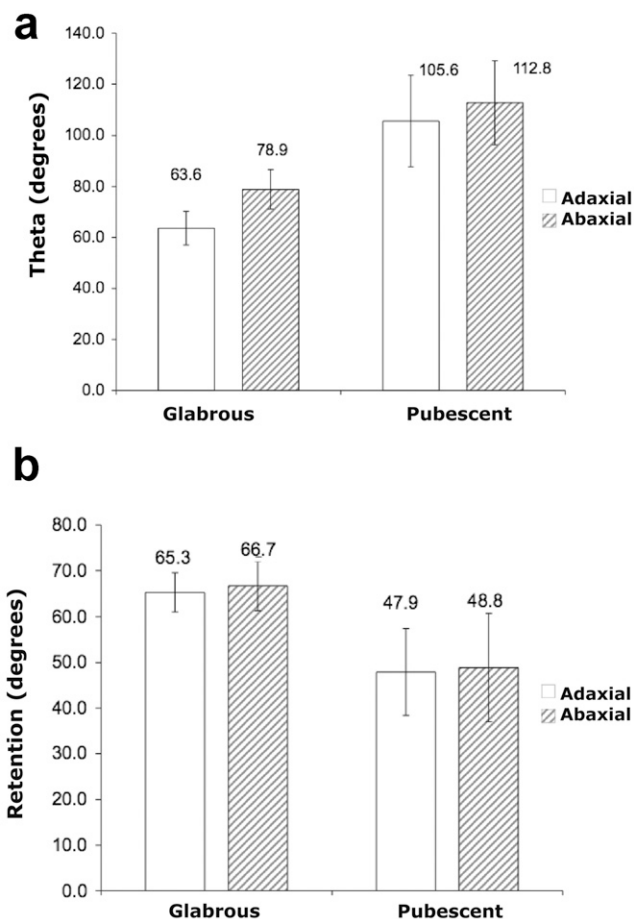


Fig. 3 Droplet contact angle θ (a) and droplet retention (b) for glabrous and pubescent leaves. Open bars represent adaxial surfaces, and hatched bars represent abaxial surfaces. Differences in θ for glabrous leaves significant at $P < 0.05$.

Table 3

Summary Values for Abaxial Surface Characteristics between Habitat Types

Habitat	θ	Retention	Stomatal density	Guard cell length	Stomatal pore length	Stomatal index
Steppe	153.3 (15.0)	28.8 (14.7)	124.8 (15.5) ^a	22.0 (.9) ^a	15.0 (1.4) ^a	1.9 (.3) ^a
Ecotone	86.0 (9.7)	68.4 (4.3)	199.2 (21.8)	33.5 (2.0)	21.9 (1.6)	5.9 (.6)
Temperate rain forest	68.7 (7.6)	69.3 (1.9)	234.4 (16.6)	28.9 (1.0)	16.9 (.7)	6.2 (.4)

Note. Data are means \pm SE.

^a Data represent one species only because of difficulty of extracting a surface cast from highly pubescent leaves or leaves with stomatal crypts.

Interestingly, leaves in temperate rain forest habitats were not well adapted to minimizing the amount of surface area in contact with liquid water. Plants in these habitats had the most wettable leaves (low values of θ) and the highest levels of droplet retention. Neinhuis and Barthlott (1997) reported that water-repellent leaves were nearly completely absent in evergreen tropical forests. Leaves of rain forest species typically were nonwaxy, and they suggested that wettable leaves were more common in these habitats because leaves remained on trees for several years under conditions that were unfavorable for maintaining epicuticular waxes. In regions with high annual precipitation, fragile waxes that are eroded from leaf surfaces during frequent rainfall events may not be replaced after leaves are fully expanded, resulting in leaves that become more wettable over their several-year life span. However, in our study, we do not have data on the wax characteristics of cuticles.

Past studies have documented some disadvantages in having wettable leaves. In addition to increased susceptibility to pathogen infection (e.g., Butler 1996; Bradley et al. 2003), many studies have reported negative influences on photosynthesis, growth, and reproduction (e.g., Brewer and Smith 1994; Ishibashi and Terashima 1995; Hanba et al. 2004). For example, Letts and Mulligan (2005) reported reductions in leaf-level net photosynthesis by abaxial leaf wetness in some species in a lower montane cloud forest in Colombia. They attributed this result to low levels of ambient photosynthetically active radiation that were further reduced at the leaf level by surface moisture. In this type of habitat, trade-offs related to light availability, nutrient acquisition, and temperature may have a greater influence on photosynthesis than leaf surface wetness, which in turn may limit investments in surface features related to shedding water. Additional studies are needed to test this hypothesis.

A suite of leaf surface traits related to minimizing leaf wetness (low droplet retention, high contact angles, trichomes) was especially common in plant species from drier habitats, resulting in relatively nonwettable leaves for plants in these dry habitats. Neinhuis and Barthlott (1997) also reported the highest incidence of nonwettable leaves in their study from species in xeric habitats. Like other species in dry, open habitats (Brewer and Smith 1997), the presence of leaf trichomes had a particularly strong influence on the formation, repulsion, and location of surface water on species in the arid Patagonian steppe and dry woodlands. In addition to their important favorable influences on thermal budgets of leaves

and light reflection in arid habitats with high incident solar radiation (Smith and Nobel 1977; Ehleringer and Mooney 1978), foliar trichomes also may influence photosynthesis in these habitats by limiting interference of surface moisture with photosynthetic gas exchange when plants begin the day with radiational or distillation dewfall on leaf surfaces (Brewer and Smith 1997). However, it also may influence foliar uptake of water and control of water loss, since it is possible that leaves in water-limited habitats may absorb some water through their leaves (Yates and Hutley 1995; Burgess and Dawson 2004).

The findings from this study and from many others indicate broad patterns of leaf surface characteristics related to leaf wettability. Habitats found in the rain shadow of the Andes present a useful system for examining morphological variation along a significant moisture gradient that can be defined across a relatively narrow area. Meteorological conditions leading to leaf surface wetness during the growing season are common from the wet temperate rain forests (rain, fog, cloud mist) to the arid shrub steppe (rain, radiational dewfall) in southwestern Argentina, as well as most locations in the world. Species along this gradient respond to leaf surface moisture in a variety of ways, from being completely wettable (temperate rain forest), to repelling spherical droplets from the leaf (shrub steppe). Additional comparative studies are needed to understand fully the degree of convergence among surface characteristics related to leaf wettability in similar habitats around the world, the trade-offs involved, and the specific influences on plant physiology, especially water balance and CO₂ uptake.

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