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Leaf water repellency of species in Guatemala and Colorado (USA) and its significance to forest hydrology studies

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Summary Fog persistency and high precipitation totals contribute to the unique ecohydrology of tropical montane cloud forests. The persistence of water droplets on leaf surfaces in cloud forests inhibits photosynthetic carbon exchange because carbon dioxide diffuses slower in water than air. Adaptations that reduce water retention on leaf surfaces may increase photosynthetic capacity of cloud forests. The objective of the present study was to determine if 12 cloud forest species from the Sierra de las Minas, Guatemala have a higher degree of leaf water repellency than 12 species from tropical dry forests in Chiquimula, Guatemala and 12 species from foothills–grassland vegetation in Colorado (USA). Leaf water repellency was measured as the contact angle between the leaf surface and the line tangent to the water droplet passing through the point of contact between the droplet and the leaf surface. Analysis of variance indicated that leaf water repellency was significantly different between the three study areas; however, the leaf water repellency of 12 species in the Sierra de las Minas was lower than 12 species in Chiquimula and lower than the leaf water repellency of 12 species in Colorado. Leaf water repellency of abaxial surfaces of all species in the cloud forest (Sierra de las Minas) was greater leaf water repellency of adaxial surfaces. The low values of leaf water repellency in cloud forest species may be influenced by presence of epiphylls or the loss of epicuticular wax on the leaf surfaces because of high precipitation totals and longer leaf life-span. High leaf water repellency in dry climates may be an adaptation to increase hydrological inputs underneath the canopy.

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Introduction

The repellency of a water droplet by a leaf surface (leaf water repellency) is a common adaptation among plant species in habitats exposed to daily precipitation during the summer growth period (Smith and McClean, 1989; Brewer and Smith, 1997; Pierce et al., 2001; Müller and Riederer, 2005). The selective pressure for reducing the wettability of leaf surfaces is thought to be physiologically driven (Smith and McClean, 1989; Brewer et al., 1991; Bradley et al., 2003). Water droplets that cover large areas of leaf surfaces restrict photosynthetic carbon exchange because carbon dioxide diffuses approximately 10,000 times slower in water than air, and the beading of water on leaf surfaces may increase the maintenance of high photosynthetic rates as less leaf area is covered with water droplets (Smith and McClean, 1989; Brewer et al., 1991; Bradley et al., 2003).

Leaf water repellency is measured by calculating the contact angle between a droplet of water and a leaf surface (Fogg, 1947; Adam, 1963; Crisp, 1963; Martin and Juniper, 1970; Smith and McClean, 1989; Bradley et al., 2003). A greater contact angle indicates a more spherical water droplet and a more water-repelling surface (Fig. 1). Several studies have found that the contact angles between a leaf surface and a water droplet ranges from 89° to 150° depending on the species and the chemical properties of the leaves (Adam, 1963; Martin and Juniper, 1970; Juniper and Jeffrey, 1983). Leaf surfaces producing contact angles exceeding 150° may not be true surfaces, but the droplet is held away from the surface by large numbers of projections of wax or trichomes (Challen, 1962; Holloway, 1970; Juniper and Jeffrey, 1983; Brewer et al., 1991; Pomeau and Villermaux, 2006). A contact angle exceeding 130° indicates leaf surfaces that are nonwetable, or repellent, and leaves with contact angles $<110^\circ$ are considered wettable, or nonrepellent (Smith and McClean, 1989; Bradley et al., 2003).

Leaf water repellency may be an important variable that influences canopy storage capacity during a rainfall event. Several studies have addressed the influence of canopy architecture, bark structure, and precipitation characteristics on canopy storage (Voigt and Zwolinski, 1964; Leonard, 1967; Aston, 1979; Hall, 1985; Herwitz, 1985; Crockford and

Richardson, 2000; Xiao et al., 2000; Levia and Herwitz, 2005), but few studies have directly addressed how leaf structure influences canopy storage capacity (Crockford and Richardson, 1990). Species with high leaf water repellency may reduce canopy storage capacity, and therefore, may decrease interception. Interception accounts for approximately 10–25% of annual precipitation depending on evaporation rates, rainfall characteristics, and vegetation (Chang, 2006). An additional variable that may explain part of this variation is leaf water repellency.

This study examined leaf water repellency between species to investigate whether leaf water repellency is an important variable that may influence canopy storage capacity. This study examined differences between leaf water repellency of common species at three research sites with distinct ecosystems (Sierra de las Minas Biosphere Reserve in Guatemala, San Jose La Arada in Guatemala, and Colorado in the USA). The objectives of this study were to determine if leaf water repellency differs between the three sites and to discuss the significance of leaf water repellency as a contributor to the hydrological flux from the canopy.

Materials and methods

Study areas

The first study area was located in the Sierra de las Minas, Guatemala approximately 5 km south of the municipality of Purulhá, Baja, Verapaz ($15^\circ 12'N$, $90^\circ 12'W$) at an elevation of 2300 m. The dominant forest type in the Sierra de las Minas was lower montane cloud forest with a high diversity of plant and animal life (Campbell, 1982; Ack and Lehnhoff, 1992; Lehnhoff and Núñez, 1998). Nightly low temperatures range from 5 to $15^\circ C$, regardless of season, and precipitation can exceed 5000 mm (Holder, 2006). Precipitation is highly variable in the Sierra de las Minas (Brown et al., 1996; Campbell, 2001). The rainy season begins in May and continues to October during which time areas can receive over 80% of their annual precipitation (Holder, 2003, 2004). Because evaporation rates are lower in the cooler months of the dry season, the persistent fog may fill canopy storages to a greater degree in the dry season. Cloud forests in the Sierra de las Minas are hydrologically different from the lowland vegetation in the surrounding valleys because cloud forest vegetation passively collects water from passing fog (LaBastille and Pool, 1978; Holder, 2006).

The second study area was in the Department of Chiquimula, Guatemala approximately 75 km southeast of the Sierra de las Minas site. Species were selected from the tropical dry forests in the municipalities of Chiquimula and San Jose La Arada ($14^\circ 45'N$, $89^\circ 30'W$) at an elevation of approximately 400 m. Annual precipitation is 1050 mm, 85% of which occurs during the rainy season from May to October. Mean monthly temperature ranges from $22.2^\circ C$ in January to $26.6^\circ C$ in May.

The third study area was located near the campus of the University of Colorado at Colorado Springs, USA ($38^\circ 53'N$, $104^\circ 48'W$) at an elevation of 2050 m. Colorado Springs lies on the boundary between highland prairie and mixed conifers in a foothills-prairie ecosystem. Annual precipitation

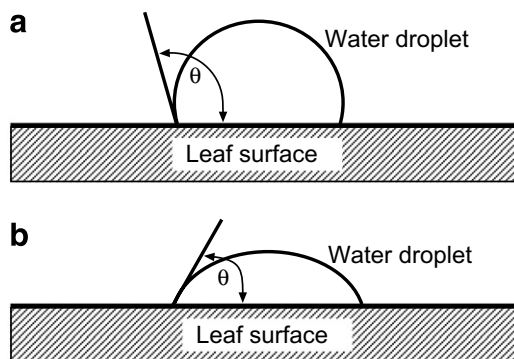


Figure 1 Leaf water repellency is measured as the contact angle (θ) between the leaf surface and the line tangent to the water droplet passing through the point of contact between the droplet and the leaf surface in this comparison of a highly repellent leaf surface (a) and a less repellent leaf surface (b).

is 442 mm. Mean monthly temperature ranges from -2.2°C in January to 20.9°C in July.

Selection of species and leaf sampling

Twelve species at each study area were selected for this study (Table 1). These species were selected because more than one representative mature individual for each species was located at the study site and because each species were common at each study area. The cloud forest species of the Sierra de las Minas were on a privately owned tract of forest adjacent to the Mario Dary Reserve. Species from Chiquimula and Colorado were sampled from isolated individuals on privately owned property. Although not all of the species are native to the study areas, all of the species have adapted to their present environments. The life-forms for the majority of the species were trees (Table 1). All of the species selected in Colorado were deciduous, all but one species selected in the cloud forest was evergreen,

and seven of the 12 species in Chiquimula were deciduous (Table 1). For each species approximately 60 leaves were collected in the field with an Azel tree pruning pole saw with aluminum telescoping poles. Leaf samples with this method can be taken from a height of approximately 10 m. An equal sample of sun leaves and shade leaves from each representative species was collected to provide a representative sample of leaf types from the canopy. Leaves were pooled together in the field during sampling, and the measurements for leaf water repellency were not recorded based on the classification of sun leaves and shade leaves.

Leaf water repellency

Leaf water repellency of the leaf samples were measured by calculating the contact angle between a water droplet and the leaf surface following the procedures of Fogg (1947), Smith and McClean (1989), Brewer et al. (1991) and Bradley et al. (2003). The leaf surface was dried with a nonabrasive

Table 1 Species at each study area selected for this study

Location	Species	Leaf habit	Life-form
Colorado, USA	<i>Acer saccharinum</i> L.	Deciduous	Tree
	<i>Catalpa speciosa</i> Warder ex. Engelm.	Deciduous	Tree
	<i>Fraxinus pennsylvanica</i> Marsh.	Deciduous	Tree
	<i>Gleditsia triacanthos</i> L.	Deciduous	Tree
	<i>Helianthus annuus</i> L.	Deciduous	Herb
	<i>Philadelphus coronarius</i> L.	Deciduous	Shrub
	<i>Populus tremuloides</i> Michx.	Deciduous	Tree
	<i>Prunus x cistena</i> (N.E. Hansen) Koehne	Deciduous	Shrub
	<i>Quercus gambelii</i> Nutt.	Deciduous	Tree
	<i>Syringa vulgaris</i> L.	Deciduous	Shrub
	<i>Ulmus pumila</i> L.	Deciduous	Tree
	<i>Verbesina encelioides</i> (Cav.) Benth. & Hook.	Deciduous	Herb
Sierra de las Minas, Guatemala	<i>Alnus arguta</i> (Schltdl.) Spach	Evergreen	Tree
	<i>Casimiroa edulis</i> La Llave & Lex.	Evergreen	Tree
	<i>Cecropia obtusifolia</i> Bertol.	Evergreen	Tree
	<i>Cyathea divergens</i> Kunze var. <i>tuerckheimii</i> (Maxon) Tryon	Evergreen	Tree fern
	<i>Geonoma undata</i> Klotzsch	Evergreen	Palm
	<i>Liquidambar styraciflua</i> L.	Deciduous	Tree
	<i>Persea</i> sp.	Evergreen	Tree
	<i>Psidium guajava</i> L.	Evergreen	Tree
	<i>Solanum aphyodendron</i> S. Knapp	Evergreen	Treelet
	<i>Talauma mexicana</i> (DC.) G. Don	Evergreen	Tree
	<i>Tibouchina urvilleana</i> (DC.) Cogn.	Evergreen	Shrub
	<i>Viburnum</i> sp.	Evergreen	Shrub
Chiquimula, Guatemala	<i>Annona squamosa</i> L.	Deciduous	Tree
	<i>Caesalpinia velutina</i> (Britton & Rose) Standl.	Deciduous	Tree
	<i>Crescentia cujete</i> L.	Evergreen	Tree
	<i>Gliricidia sepium</i> (Jacq.) Kunth ex. Walp.	Deciduous	Tree
	<i>Guazuma ulmifolia</i> Lam.	Deciduous	Tree
	<i>Mangifera indica</i> L.	Evergreen	Tree
	<i>Melia azedarach</i> L.	Deciduous	Tree
	<i>Salix humboldtiana</i> Willd.	Evergreen	Tree
	<i>Swietenia humilis</i> Zucc.	Deciduous	Tree
	<i>Tabebuia pentaphylla</i> (L.) Hemsl.	Deciduous	Tree
	<i>Tamarindus indica</i> L.	Evergreen	Tree
	<i>Tecoma stans</i> (L.) Juss. ex Kunth	Evergreen	Tree

absorbent filter paper and was pinned onto a balsa wood platform to flatten the leaf surface to view the leaf's horizontal profile. A 10 μ l droplet of distilled water was placed onto 30 adaxial and 30 abaxial leaf surfaces with an Eppendorf micropipette for a total of 60 different leaves from each species. A photograph of a profile of the water droplet resting on the leaf surface was taken with a Nikon D70 digital camera with a 105MM F/2.8 D AF Micro-Nikkor lens. The digital photographs were downloaded into Adobe Photoshop. From the computer image, the contact angle of the leaf surface and the line tangent to the droplet through the point of contact was measured with Scion Image software (Fig. 1). In all cases, contact angles were measured relative to the horizontal leaf surface even when droplets rest above the surface on epidermal projections such as leaf hairs.

Data analysis

A two-tailed *t* test was conducted to determine if significant differences in leaf water repellency occurred between adaxial and abaxial surfaces for each species. A nested analysis of variance was used to test whether there were significant differences in leaf water repellency in the 36 species and between the three sites. Species were nested within sites, leaves were nested within species, and leaf surfaces were nested within leaves. When analysis of variance indicated significant differences among species and sites, Tukey HSD multiple comparisons tests were performed to determine which pairs of species exhibited significant differences. A given effect was assumed significant at $p < 0.05$. All statistical analysis was conducted with Systat 11 (Systat Software Inc., Richmond, CA).

Results

Leaf water repellency was significantly greater on the abaxial surface than on the adaxial surface for 22 species (Table 2; *t*-test, $p < 0.05$). Eight species had greater leaf water repellency on the adaxial surface than on the abaxial surface, but in only two of these cases were the differences significant (Table 2). Leaf water repellency on abaxial surfaces ranged widely from 47.11° (*Ulmus pumila* in Colorado) to 144.25° (*Caesalpinia velutina* in Chiquimula). The values for leaf water repellency also ranged widely on adaxial surfaces. Leaf water repellency on adaxial surfaces ranged from 40.33° (*Cecropia obtusifolia* in the Sierra de las Minas) to 125.36° (*Annona squamosa* in Chiquimula).

Based on the criteria of Crisp (1963), a contact angle exceeding 130° indicates leaf surfaces that are nonwetable, or repellent, and leaves with contact angles <110° are considered wettable, or nonrepellent. Leaf water repellency of abaxial surfaces for five species was greater than 130°. Leaf water repellency of the adaxial surface for 34 species and of the abaxial surface for 23 species was less than 110°.

Species in Colorado generally had higher values of leaf water repellency than the Sierra de las Minas and Chiquimula. Analysis of variance found differences in leaf water repellency between the three sites, between the 36 species, and between the 36 species broken down into leaf surface

(Table 3; $p < 0.001$). Based on the Tukey HSD multiple comparison test, leaf water repellency between the three sites differed. Results from the analysis of variance of the 12 species within each study area showed significant differences between species and between adaxial and abaxial leaf surfaces (Table 3; $p < 0.001$).

Discussion

Leaf water repellency was greater in the drier sites of Colorado and Chiquimula than the cloud forest of the Sierra de las Minas. This result was not expected based on the hydrological uniqueness of cloud forests. Cloud forests in the Sierra de las Minas are hydrologically different from the lowland vegetation in the surrounding valleys because cloud forest vegetation passively collects water from passing fog (Holder, 2004, 2006). Fog precipitation occurs when fog droplets pass through the canopy of the forest and are filtered by vegetative surfaces producing persistently high canopy storage capacities. The intercepted fog droplets coalesce on the vegetative surfaces and drip to the forest floor. Fog precipitation is common in these montane forests at elevations from 840 to 3475 m (LaBastille and Pool, 1978). Additionally, epiphytes in cloud forest may play a significant role in interception by increasing canopy storage capacity (Veneklaas and van Ek, 1990; Fleischbein et al., 2005). Cloud forests have a high water storage capacity because of high precipitation totals, fog persistency, and epiphytic growth. With a large quantity of canopy storage, an adaptation to allow the water to bead on the leaf surface to maximize gas exchange for photosynthesis and to increase productivity was predicted.

Photosynthesis and productivity was limited when abaxial surfaces were wet in lower montane cloud forests of Colombia (Letts and Mulligan, 2005). All of the species in the Sierra de las Minas had higher values of leaf water repellency on the abaxial surface than on the adaxial surface compared with seven of 12 species in Chiquimula and nine of 12 species in Colorado (Table 2). The majority of stomata were present on the abaxial surface of the leaves of the species in this study. Although cloud forest species had lower leaf water repellency, these species had higher values for leaf water repellency on the abaxial surface relative to the adaxial surface. The relatively higher leaf water repellency for abaxial leaf surfaces in cloud forest species compared with the drier sites of Chiquimula and Colorado may be compensation for persistently wet leaf surfaces in the cloud forests.

Several tropical cloud forest plant species have developed drip tips to channel water off the leaf surface. Although drip tips affect the drainage of water from the leaf surface, drip tips do not prevent the establishment and growth of epiphyllous lichens (Lücking and Bernecker-Lücking, 2005). Epiphytic microorganisms (filamentous fungi, yeasts, and bacteria) influence the wetting properties of leaf surfaces and may affect leaf water repellency (Bunster et al., 1989; Knoll and Schreiber, 1998, 2000). The presence of microscopic epiphylls in the cloud forest species of the Sierra de las Minas may have decreased leaf water repellency in the cloud forest compared to the drier sites of Chiquimula and Colorado where epiphylls are not as common.

Table 2 Leaf water repellency (in degrees) for 36 species

Species ^a	Adaxial surface		Abaxial surface	
	Mean	SD	Mean	SD
Colorado, USA				
<i>Acer saccharinum</i> ***	73.23	15.27	134.55	6.28
<i>Catalpa speciosa</i> ***	81.67	15.74	124.27	10.78
<i>Fraxinus pennsylvanica</i> ***	73.75	11.78	91.92	14.50
<i>Gleditsia triacanthos</i> ***	59.73	10.04	71.91	9.06
<i>Helianthus annuus</i>	55.20	12.71	57.22	11.23
<i>Philadelphus coronaries</i>	78.26	18.47	71.81	11.14
<i>Populus tremuloides</i>	115.46	24.56	123.69	11.52
<i>Prunus x cistena</i> ***	102.98	17.05	124.91	12.78
<i>Quercus gambelii</i> ***	71.70	7.28	120.71	15.18
<i>Syringa vulgaris</i> **	76.65	12.55	54.12	13.23
<i>Ulmus pumila</i>	51.02	13.02	47.11	10.99
<i>Verbesina encelioides</i> ***	91.33	15.18	128.28	9.32
Sierra de las Minas, Guatemala				
<i>Alnus arguta</i> ***	51.81	10.22	103.96	23.34
<i>Casimiroa edulis</i> ***	47.72	10.19	122.41	25.75
<i>Cecropia obtusifolia</i> **	40.33	7.24	57.87	17.21
<i>Cyathea divergens</i>	53.91	7.28	No data	No data
<i>Geonoma undata</i>	51.97	8.46	56.86	13.52
<i>Liquidambar styraciflua</i> ***	58.35	10.15	74.38	11.74
<i>Persea</i> sp.***	52.73	7.70	75.46	15.59
<i>Psidium guajava</i> ***	53.78	12.41	84.81	28.43
<i>Solanum aphyodendron</i> ***	46.56	8.67	135.04	7.83
<i>Talauma mexicana</i> *	40.45	10.09	48.50	13.25
<i>Tibouchina urvilleana</i> ***	58.27	11.83	98.33	25.88
<i>Viburnum</i> sp.***	52.18	8.09	70.78	5.56
Chiquimula, Guatemala				
<i>Annona squamosa</i>	125.36	19.48	130.72	9.79
<i>Caesalpinia velutina</i> ***	108.93	22.18	144.25	7.06
<i>Crescentia cujete</i> **	59.80	8.97	52.51	9.26
<i>Gliricidia sepium</i> ***	92.00	24.33	138.81	7.62
<i>Guazuma ulmifolia</i> ***	57.17	7.93	112.20	23.35
<i>Mangifera indica</i>	61.54	6.11	64.97	7.78
<i>Melia azedarach</i> *	57.91	8.86	63.35	8.41
<i>Salix humboldtiana</i>	68.55	8.02	64.82	13.14
<i>Swietenia humilis</i> ***	54.30	9.21	64.57	12.63
<i>Tabebuia pentaphylla</i>	66.98	5.02	66.53	6.28
<i>Tamarindus indica</i>	78.66	17.32	74.29	20.91
<i>Tecoma stans</i>	60.15	5.65	58.08	6.80

^a Adaxial and abaxial leaf surfaces were significantly different at $p < 0.05$ (*); $p < 0.01$ (**); $p < 0.001$ (***)

Leaf structure and leaf surface chemistry also influence leaf water repellency. Plant surfaces are water repellent because of three dimensional microstructures of the epidermal cells and hydrophobic wax crystals (Challen, 1960; Holloway, 1969, 1970; Wagner et al., 2003; Neinhuis and Barthlott, 1997, 1998; Beattie and Marcell, 2002; Koch et al., 2006; Shirtcliffe et al., 2006). Leaves with trichomes were more water repellent than leaf surfaces without trichomes (Brewer et al., 1991). Species with water-repellent leaf surfaces had the lowest retention of particles such as dust (Neinhuis and Barthlott, 1997, 1998). Neinhuis and Barthlott (1997) found that water-repellent leaves are almost absent in evergreen tropical forests due to the fact

that the leaves remain on the plants for up to several years under environmental conditions unfavorable for the maintenance of epicuticular waxes. High annual precipitation as experienced in cloud forest environments has an erosive effect on the waxes of leaves that persist in the canopy for greater than one year (Baker and Hunt, 1986). The loss of epicuticular wax because of high precipitation totals may explain the lower leaf water repellency in cloud forest species than in Chiquimula and Colorado.

Additionally, leaf water repellency decreased with the age of the leaf because of the deterioration of epicuticular waxes (Cape, 1983, 1988; Crockford and Richardson, 1990; Kupcinskiene and Huttunen, 2005). Because all of the species

Table 3 Within-site differences in leaf water repellency for each leaf surface assessed with a one-way analysis of variance

Site	Variable	Source of variation	MS	df	F	P
All	Leaf water repellency (θ)	Location Error	71,238.1 914.9	2 2028	77.864	0.001
All	Leaf water repellency (θ)	Species Error	32,463.1 431.9	35 1995	75.159	0.001
All	Leaf water repellency (θ)	Species/surface Error	23,392.6 183.9	70 1960	127.215	0.001
Sierra de las Minas	Leaf water repellency (θ)	Species Error	11,485.7 595.9	11 603	19.292	0.001
Sierra de las Minas	Leaf water repellency (θ)	Adaxial leaf surface Error	928.2 88.4	11 305	10.505	0.001
Sierra de las Minas	Leaf water repellency (θ)	Abaxial leaf surface Error	19,579.5 327.5	10 287	59.779	0.001
Chiquimula	Leaf water repellency (θ)	Species Error	43,940.0 312.9	11 686	140.448	0.001
Chiquimula	Leaf water repellency (θ)	Adaxial leaf surface Error	15,392.7 184.5	11 341	83.447	0.001
Chiquimula	Leaf water repellency (θ)	Abaxial leaf surface Error	35,086.7 154.1	11 333	227.743	0.001
Colorado	Leaf water repellency (θ)	Species Error	34,903.6 407.578	11 706	85.637	0.001
Colorado	Leaf water repellency (θ)	Adaxial leaf surface Error	10,581.2 227.3	11 347	46.553	0.001
Colorado	Leaf water repellency (θ)	Abaxial leaf surface Error	33,683.0 133.7	11 347	251.951	0.001

in Colorado were deciduous, the sampled leaves from the Colorado species may not have weathered as greatly as the evergreen species from the Sierra de las Minas (Table 1).

Leaf water repellency in the drier sites of Colorado and Chiquimula may be greater as a functional response to increase the removal of water from the canopy to increase soil moisture and improve the water balance for the plant. Species with highly repellent leaf surfaces may increase the quantities of throughfall, stemflow, and fog precipitation at a site and may result in greater hydrological inputs beneath the canopy in water stressed environments. If the leaf water repellency of dominant species of an ecosystem is large, then the water balance in the ecosystem may be influenced by leaf water repellency. Because species from Colorado and Chiquimula have highly water-repellent leaf surfaces, the added hydrological inputs from highly repellent leaves may improve the water balance for vegetation in these water stressed regions. Alternatively, the potentially larger hydrological inputs underneath the canopy of species with highly repellent leaves may be a side effect of leaf trait (deciduous vs. evergreen) as older leaves lose their ability to repel water rather than an adaptation to limited water resources.

Leaf water repellency measured in this study was not necessarily equivalent to leaf hydrophobicity, or how easily water drains off a leaf surface. A leaf with a high repellency

does not necessarily mean that the water droplet will roll off the leaf surface (McHale et al., 2004; Shirtcliffe et al., 2006). Factors that influence the movement of water off a leaf surface include the leaf inclination angle and the microstructure of the leaf surface.

Vegetation changes in which native species are cleared for introduced or early successional species (i.e. agriculture, plantation forestry, selective logging, etc.) may impact the hydrological processes of cloud forests and may reduce water resources of the surrounding arid valleys of Sierra de las Minas (Holder, 2006). Very limited details are known about the foliar ecology and the canopy storage capacities of the tropical cloud forest species that are being altered by humans. Hydrological inputs and site water balance may be connected to differences between leaf water repellency of native species and introduced species. The significance of leaf water repellency and leaf hydrophobicity as a mechanism that influences hydrological processes in forest ecosystems are unexplored variables, and further investigation of these mechanisms will need to be conducted to determine if leaf water repellency is a significant variable. Improved models of forest hydrology processes may be formulated that incorporate leaf surface variables with better understanding of differences in leaf water repellency among dominant species at a site and between sites.

Conclusions

Leaf water repellency was lower in cloud forest species of the Sierra de las Minas than in the tropical dry forest species of Chiquimula and the grassland–foothills species of Colorado. Species in Colorado generally had the largest leaf water repellency. Adaxial surfaces were less repellent than abaxial surfaces in all of the species in the cloud forest. Adaxial surfaces were less repellent in nine of the 12 species in Colorado and seven of the 12 species in Chiquimula. The significance of leaf water repellency and leaf hydrophobicity as a mechanism that influences hydrological processes in forest ecosystems are unexplored variables, and further investigation of these mechanisms will need to be conducted.

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