HYDROLOGICAL PROCESSES
Hydrol. Process. (2007)
Published online in Wiley InterScience
(www.interscience.wiley.com) DOI: 10.1002/hyp.6844

Fog interception by non-vascular epiphytes in tropical montane cloud forests: dependencies on gauge type and meteorological conditions

Juan Camilo Villegas[1,2]* Conrado Tobón[3] and David D. Breshears[2,4,5]

[1] *Grupo GIGA, Universidad de Antioquia, Medellín, Colombia*
[2] *School of Natural Resources, University of Arizona, Tucson, AZ, USA*
[3] *Universidad Nacional de Colombia-Sede Medellín. Medellín, Colombia*
[4] *Institute for the Study of the Planet Earth, University of Arizona, Tucson, AZ, USA*
[5] *Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA*

Abstract:

Precipitation is the most fundamental input of water for terrestrial ecosystems. Most precipitation inputs are vertical, via rain, but can be horizontal, via wind-driven rain and snow, or, in some ecosystems such as tropical montane cloud forests (TMCFs), via fog interception. Fog interception can be particularly important in ecosystems where fog is frequently present and there are seasonal periods of lower rainfall. Epiphytes in trees are a major ecological component of TMCFs and are particularly dependent on fog interception during periods of lower rainfall because they lack access to soil water. But assessing fog interception by epiphytes remains problematic because: (i) a variety of field or laboratory methods have been used, yet comparisons of interception by epiphytes versus interception by various types of fog gauge are lacking; (ii) previous studies have not accounted for potential interactions between meteorological factors. We compared fog interception by epiphytes with two kinds of commonly used fog gauges and developed relations between fog interception and meteorological variables by conducting laboratory experiments that manipulated key fog characteristics and from field measurements of fog interception by epiphytes. Fog interception measured on epiphytes was correlated with that measured from fog gauges but was more than an order of magnitude smaller than the actual measurements from fog gauges, highlighting a key measurement issue. Our laboratory measurements spanned a broad range of liquid water content (LWC) values for fog and indicate how fog interception is sensitive to an interaction between wind speed and LWC. Based on our results, considered in concert with those from other studies, we hypothesize that fog interception is constrained when LWC is low or high, and that fog interception increases with wind speed for intermediate values of LWC—a net result of deposition, impaction, and evaporation processes—until interception begins to decrease with further increases in wind speed. Copyright © 2007 John Wiley & Sons, Ltd.

KEY WORDS fog interception; non-vascular epiphytes; tropical montane cloud forest; fog gauges; fog chamber; Colombia

Received 16 August 2006; Accepted 12 June 2007

INTRODUCTION

The hydrological process of precipitation is the most fundamental input of water for terrestrial ecosystems. Most precipitation inputs are vertical, via rain, but in some ecosystems the precipitation inputs can be horizontal via wind-driven rain and snow or via fog interception (González, 2000; Bruijnzeel *et al.*, 2005). Horizontal precipitation via fog interception is a notably important source of water for a variety of ecosystems, from temperate evergreen forests growing in subhumid seasonal climates, such as the redwoods in California (Dawson, 1998; Burgess and Dawson, 2004), to tropical montane cloud forests (TMCFs) that have seasonally low rainfall (Bruijnzeel and Proctor, 1995; Bruijnzeel, 2001). Notably, TMCFs are classified relative to frequency of contact with fog (Bruijnzeel and Proctor, 1995; Bruijnzeel *et al.*, 2005). Fog interception represents a substantial fraction of average annual water income in most TMCFs, ranging over an order of magnitude from ~6% to 60%, with larger fractions being associated with drier ecosystems (Cavelier *et al.*, 1996; González, 2000). A major vegetation component of TMCFs is aerial epiphyte communities, which grow in association with tree structures, such as branches and stems, and enhance interception of fog and rainfall interception (Hamilton *et al.*, 1995; Clark *et al.*, 1998; Jarvis, 2000; Foster, 2001; Hölscher *et al.*, 2004). Epiphytes have a particularly important influence on fog interception in TMCFs because not only are they abundant, but they also have a high water storage capacity, can release water slowly, and their responses to evaporation and precipitation dynamics differ from those of other structural components of the forest (Veneklaas *et al.*, 1990; Richardson *et al.*, 2000). Although epiphytes represent one of the largest vegetation components of the ecosystem, they do not have direct access to soil water as other plants do and, hence,

---

*Correspondence to: Juan Camilo Villegas, 325 Biological Science Building East, University of Arizona, 1311 E 4th Street, Tucson, AZ 85721 USA. E-mail: villegas@email.arizona.edu

are particularly dependent on fog interception (Benzing, 1998). The epiphyte community commonly includes vascular plants (such as orchids, ferns and bromeliads) and non-vascular species (such as mosses, which are generally the most abundant, lichens) and liverworts (Frahm, 1990; Wolf, 1996; Bruijnzeel, 2001). The diversity of epiphytes in some of these ecosystems has been reported to be comparable to the combined diversity of lowland rainforest trees and herbs (Hamilton *et al*., 1995; Nieder *et al*., 2001).

In the process of fog interception, the small water droplets that form the fog are transported by wind and intercepted by vegetation structures such as leaves, branches and epiphytes to form bigger drops that can either be precipitated onto the forest floor or evaporated back to the atmosphere (Kerfoot, 1968). Because fog occurs under conditions of high relative humidity and low solar radiation, water intercepted from fog is less likely to be evaporated, yielding additional precipitation through subsequent dripping of intercepted fog to the forest floor (Hamilton *et al*., 1995; González, 2000). Fog interception is influenced by several meteorological variables, including fog liquid water content (LWC), fog drop size, wind speed and direction, and duration and frequency of fog events (Bruijnzeel and Proctor, 1995; Bruijnzeel *et al*., 2005). Although these variables likely interact to influence fog interception, few studies have explicitly evaluated such interactions, especially under controlled conditions (Merriam, 1973; Chang *et al*., 2002). Fog interception is also influenced by biotic variables related to structural characteristics of the forests, such as height, size, spatial pattern, orientation relative to prevailing wind direction, biomass and physical characteristics of leaves and epiphytes (Bruijnzeel *et al*., 2005). Yet systematic observations that consider both meteorological and biotic characteristics are generally lacking (Mulligan and Burke, 2005). Addressing these issues requires the use of combined laboratory and field experiments, where interrelationships among physical and biotic factors can be evaluated (Bruijnzeel, 2001).

Several different approaches have been used to estimate fog interception (Bruijnzeel *et al*., 2005), including:

1. Water and mass balance techniques, such as the wet canopy water budget approach that estimates fog interception through a comparison of net and gross precipitation for periods with and without fog; see Holwerda *et al*. (2006) for recent improvements in accounting for differences in fog interception due to evaporation, wind and topography.
2. Mass balance and isotopic techniques that trace the origin of the water that reaches the forest floor.
3. Micrometeorological methods based on the eddy covariance technique, under which exchanges of cloud water the forest and the atmosphere are estimated as the covariance between the turbulent components of vertical wind speed and LWC.
4. Using gauges designed to intercept fog, referred to as 'fog gauges'.

By far, the most common approach is the use of fog gauges; see summaries in González (2000), Jarvis (2000), Bruijnzeel (2001) and Bruijnzeel *et al.* (2005). However, estimates of fog interception based on fog gauges might not be representative of key characteristics of forest canopies that likely influence fog interception, such as epiphyte loads and morphology (Chang *et al*., 2002; Bruijnzeel *et al*., 2005; Tobón *et al*., 2006). In addition, estimates from fog gauges are often not directly comparable because many types of fog gauge have been used (Schemenauer and Cereceda, 1994; Juvik and Nullet, 1995; Bruijnzeel *et al*., 2005). Metal-louvred screen gauges have been shown to drain their catch more efficiently than wire-mesh screens. Cylindrical gauges, which are multidirectional, have been shown to be more efficient than two-dimensional screens, which are unidirectional, because the exposed area remains constant regardless of the wind direction (Juvik and Nullet, 1995). Further, the influence of wind-driven rainfall intercepted by the fog gauges is generally not differentiated from actual fog interception (Hafkenscheid, 2000; Juvik and Nullet, 1995; Cavelier *et al*., 1996; Bruijnzeel *et al*., 2005). Because of these issues related to the use of fog gauges, debate remains about how to best to estimate fog interception (Bruijnzeel *et al*., 2005).

In summary, although fog interception by vegetation in TMCFs is recognized to be an important hydrological process, assessing fog interception remains problematic because: (i) a variety of field or laboratory methods have been used, yet simultaneous comparisons of fog interception by vegetation versus interception by various types of fog gauges is lacking; (ii) previous studies have not accounted for the role of potential interactions between meteorological factors to produce responses in fog interception by vegetation. We compared fog interception by epiphytes with two kinds of commonly used fog gauge and developed relations between fog interception and meteorological variables by conducting laboratory experiments that manipulated key fog characteristics and by obtaining field measurements of fog water interception by epiphytes.

MATERIALS AND METHODS

We conducted laboratory and field studies in which we used epiphyte samples and two different kinds of fog gauge to measure fog interception. The laboratory study focused on simulations of fog interception by epiphytes in a fog simulator (fog chamber, after Jarvis (2000)) that enabled the production of fog under controlled meteorological conditions. The field study focused on measurements of fog interception for different fog events that were then compared with estimates obtained in the laboratory.

Study site

Our study site for field measurements and collection of samples for fog chamber experiments was 'La Aguada

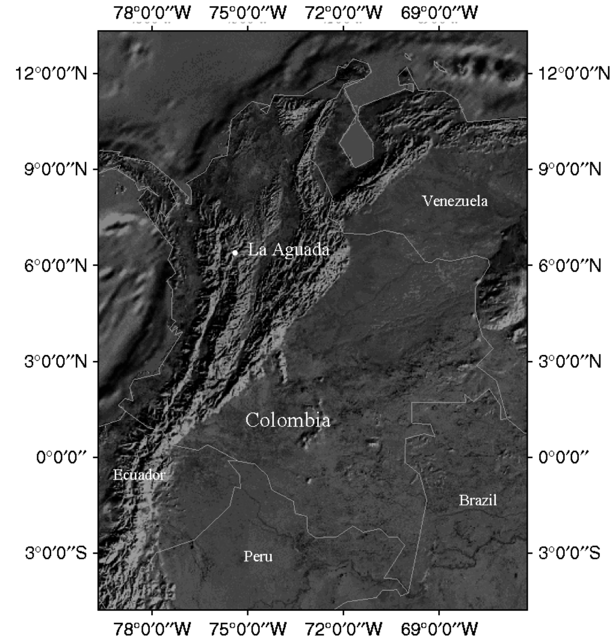

Figure 1. Location of the study area in the central Andes of Colombia (6°13′08″N, 75°30′29″W)

Figure 2. The fog chamber, a controlled volume containing two types of fog gauge: polypropylene harp (unidirectional gauge; left) and a Juvik cylinder (multidirectional gauge, right), where 21 fog events were simulated

forest’, a TMCF located in Medellín, Colombia, within Arví Regional Park (eastern flank of the Aburrá Valley and belonging to CORANTIOQUIA Environmental Corporation for the Center of Antioquia, Colombia; 6°13′08″N and 75°30′29″W). The forest spans approximately 100 ha with altitudes ranging between 2200 and 2500 m above sea level (Figure 1). Vegetation cover includes secondary forests in an advanced stage of succession, mainly composed of mid-size trees, with larger trees approaching 25 m in height and having relatively low levels of human-induced disturbance. The forest contains approximately 85 plant species, grouped into 34 families, with the families Meliaceae, Moraceae and Proteaceae being the most representative of the tree group and the families Rubiaceae and Asteraceae and Arecaceae being the most representative of the arbustive group (CORANTIOQUIA, 2005, personal communication). Fog forms frequently on most of the high ridges of the Aburrá valley (with altitudes over 2000 m above sea level), as a consequence of moist air masses from the north that condense while rising up through the mountain ridges (Mejía, 2002). Fog on the eastern slope of the valley occurs more frequently during rainless seasons and is formed especially during morning hours, when differential heating of the two flanks supports the development of convective cells that transport moist air from the bottom of the valley to its top, condensing at around 2000 m. The production of these convective cells is normally associated with early-morning conditions following cloudless, stable nights, resulting from atmospheric stationary conditions, common during rainless periods (Adarve and Molina, 1984).

Laboratory experiments

We built a fog chamber similar to (but smaller than) the one described by Jarvis (2000) (3 m long × 1·7 m height × 1·5 m wide), isolated from the exterior by a thermal polyurethane plastic (Figure 2). Fog was introduced into the chamber via a nozzle (model 23 412-1/4-20 from Spaying Systems Co.) that uses a mixture of pressurized water (for our experiments we used a constant pressure of ∼68·95 hPa) and air at variable pressures, yielding fog with droplet diameters ranging from 10 to 20 μm and flow rates ranging from 6·4 to 22 l h^{-1}. Liquid outflow for each event was determined from nozzle operation charts from the manufacturer (Spraying Systems Co., 1997) relating air and water pressure to liquid output. To estimate the relationship between air pressure and liquid outflow beyond the range of the operation charts, we directly calculated regression equations ($0{\cdot}98 < R^2 < 1{\cdot}00$, data not shown), as suggested by the manufacturer. The posterior end of the fog chamber was open, allowing circulation of air and fog and the maintenance of a constant density of fog in the chamber throughout the duration of the simulated fog events. Wind circulation and wind speed were controlled using a ventilation system installed in the chamber.

Two types of fog gauge were used in the fog chamber: a polypropylene harp (after Frumau *et al.* (2006)), referred to as ‘unidirectional’ because its interception efficiency depends on wind direction (Schemenauer and Cereceda, 1994; Bruijnzeel *et al.*, 2005), and a modified Juvik cylinder (Juvik and Ekern, 1978; Frumau *et al.*, 2006), referred to as ‘multidirectional’ because the area of exposure remains constant regardless of wind direction. The polypropylene harp consisted of a square frame (0·25 m^2) made of PVC with a series of parallel polypropylene strings (calibre 60) running every 2 mm and oriented perpendicular to the prevailing direction of the fog-carrying wind. The modified Juvik cylinder was comprised of a cylindrical, louvred aluminium screen 40 cm in height and 15 cm in diameter with a metallic mesh of 1·55 mm spacing between wires (Phifer Shadescreen, provided by J. O. Juvik; Juvik and Ekern, 1978).

For both types of gauge, the volume of water intercepted was converted into laminar units by factoring in surface area and interception efficiency of the gauge. Gauge-specific interception efficiencies were estimated using relationships reported by Frumau *et al.* (2006):

$$C_u = 0{\cdot}29C_t \times \mathrm{CWF}_u + 0{\cdot}14 \qquad (1)$$

for the unidirectional gauge, and

$$C_m = 0{\cdot}36C_t \times \mathrm{CWF}_m + 0{\cdot}2 \qquad (2)$$

for the multidirectional gauge, where C_u and C_m represent the interception efficiency for the unidirectional gauge and multidirectional gauge respectively, C_t is the normalization time factor equal to 30 divided by the duration of the measured fog event (minutes), and CWF_u and CWF_m (mm h^{-1}) are the cloud water flux measured by the unidirectional gauge and the multidirectional gauge respectively.

We installed a portable automatic weather station (AWS; Davis Weather Monitor II) in the chamber to measure temperature, relative humidity, wind vector (speed and direction) and precipitation during the simulated fog events (sampling frequency was 1 min). We calculated mean LWC for each event based on the amount of moisture (milligrams) injected to the fog chamber per unit time (seconds) and the volume of the fog chamber (cubic metres); the amount of moisture injected into the chamber was corrected for water that was intercepted by the chamber walls, which was collected and measured directly with a rain gauge.

We simulated 21 fog events in the fog chamber that represented stratified combinations of wind speed, LWC and fog event duration using ranges of values previously observed at our study site (Table I). The physical characteristics of fog simulated in the chamber were held relatively constant within each fog event to provide controlled comparisons. However, we recognize that meteorological conditions in the field can vary substantially with respect to wind speed, LWC, relative humidity, radiation and potential evapotranspiration during a single fog event. We grouped our experiments into four levels of mean wind speed (0–0·5, 0·6–1·0, 1·1–1·5, 1·6–2·0 m s^{-1}) and five levels of mean LWC (<50, 51–100, 101–150, 151–200, >200 mg m^{-3}), with each level of LWC evaluated at all four levels of wind speed.

Table I. Ranges of variation of meteorological conditions and fog events characteristics used in the 21 fog events developed in the fog chamber and observed in the six fog events monitored in the field

Variable	Fog chamber		Field experiments	
	Minimum	Maximum	Minimum	Maximum
Temperature (°C)	20·0	24·0	17·2	18·4
Relative humidity (%)	90·6	97·0	77·9	85·2
Wind speed (m s^{-1})	0·0	2·1	0·8	2·1
LWC (mg m^{-3})	22·3	221·2	10·3	69·5
Duration of the event (min)	37	121	43	215

For each fog event simulated in the chamber, fog interception was measured using both gauge types and four epiphyte samples (branches with epiphytes), all of which were placed perpendicular to the flow of fog. The epiphyte samples were branches ~50 cm long and varied in amount of epiphyte coverage, which was mostly classified as moss balls (non-vascular epiphytes), with some sporadic presence of small bromeliads.

Field measurements

Fog interception was measured in the field at La Aguada using a multidirectional fog gauge and epiphyte samples ($n = 15$ per fog event, with only 14 for one event) for six fog events that occurred during the November–December 2005 dry season. The epiphyte samples were generally placed adjacent to the multidirectional gauge and perpendicular to the main fog-carrying wind direction (commonly northwest) at a height of 2 m in an exposed, open area approximately 50 m from the edge of the adjacent forest, at 2250 m above sea level. A portable AWS (Davis Weather Monitor II) installed in the open at 2 m height monitored metrological variables (temperature, relative humidity, precipitation, and wind speed and direction) every 5 min. The duration of each fog event was also observed and recorded manually (Table I). To confirm that our estimates at 2 m were also relevant to taller tree locations, we placed an additional gauge at a height of 15 m in the forest. The amount of fog measured using the fog gauge at 15 m in the canopy was consistently within 10% of that for the gauge in the open area at 2 m; data from both heights were used to make comparisons between gauges and epiphyte interception.

We were unable to measure LWC directly in the field, so instead estimated it using a rearrangement of the relationship proposed by Tobón *et al.* (2006):

$$\mathrm{LWC} = \frac{\mathrm{FI}}{u \times \mathrm{IE} \times A} \qquad (3)$$

where FI is the fog interception, u is the product of wind speed during the fog event, IE is the interception efficiency of the device and A is the area exposed. For each fog event, we had data of fog interception, geometry and interception efficiency for the multidirectional fog gauge and of mean wind speed as recorded by the weather station.

Measurement of fog interception by epiphytes

Fog interception by epiphytes was estimated by measuring weight change. Before starting each measurement in either the field or the fog chamber, epiphyte samples were air-dried until they reached a constant weight and their basic dimensions (height and diameter) were then recorded; after each fog event, samples were reweighed. To correct for any fog intercepted directly by the branches rather than by the epiphytes, the epiphyte component was then separated from the main branch and the branches were weighed immediately after the separation, air-dried and weighed again. Bulk interception on epiphyte samples was calculated as the difference in weight prior to and following exposure to the fog (corrected for branch interception, as described above). To express the interception in laminar units, bulk interception was divided by the exposed cylindrical surface area of the sample assuming a regular cylindrical shape. Epiphyte samples did not reach saturation in any of our measurements, based on visual confirmation that water was not dripping from the samples; therefore, the amount of water stored, as measured by changes in sample weights as described above, was assumed to equal the net amount of intercepted fog.

Data analysis

Relationship between actual fog interception by epiphytes and fog gauges. To examine the relation between fog interception by epiphytes and the two types of fog gauge, two sample *t*-tests were performed to compare the amount of water intercepted by epiphyte samples with both types of fog gauge. In those cases where the *t*-tests resulted in significant differences among fog gauges and epiphytes, Type II regression analyses were performed to determine the magnitude of the differences and to define approximate relationships between fog gauge and epiphyte sample estimates while accounting for any potential error on the measurement of the independent variable (Warton *et al.*, 2006).

Fog interception and meteorological characteristics of fog events. We analysed the results from the fog chamber using a multifactor analysis of variance to explain the variation in fog interception by epiphytes as related to meteorological characteristics (relative humidity, temperature, wind speed, and LWC) and their interactions. Variables that presented statistically significant relationships with fog interception by epiphytes were further analysed in more detail.

RESULTS

Relationship between actual fog interception by epiphytes and fog gauges

Interception efficiency for both types of fog gauge was calculated according to the relationships developed by Frumau *et al.* (2006), but for a wider range of interception values (Figure 3). Interception efficiency was highly correlated with cloud water flux in both the unidirectional ($R^2 = 0{\cdot}99$, $P < 0{\cdot}001$) and multidirectional ($R^2 = 0{\cdot}83$, $P < 0{\cdot}001$) gauges.

Fog interception measured on epiphyte samples was significantly different from that measured on the unidirectional gauge ($P = 0{\cdot}01$). On the other hand, there is evidence suggestive of differences between measurements on epiphytes and the multidirectional gauge ($P = 0{\cdot}10$) after correction for interception efficiency. Fog gauges, on average, overestimate fog interception on epiphytes by a factor of 12·5 (95% confidence interval [CI]: 3·5 to 21·5) for the unidirectional gauge and of 3·2 (95% CI: 1·0 to 5·3) for the multidirectional gauge (Figure 4). Nonetheless, the amount of fog interception measured on the epiphyte samples was significantly correlated with that from both types of gauge (multidirectional gauge: $R^2 = 0{\cdot}53$, $P < 0{\cdot}01$; unidirectional gauge: $R^2 = 0{\cdot}58$, $P < 0{\cdot}01$) (Figure 5).

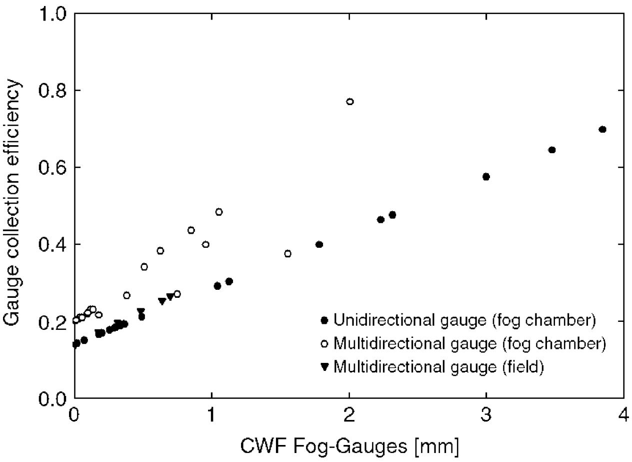

Figure 3. Calculated fog interception efficiency for the unidirectional (wire harp) and multidirectional (modified Juvik cylinder) gauges for field and laboratory measurements of fog interception

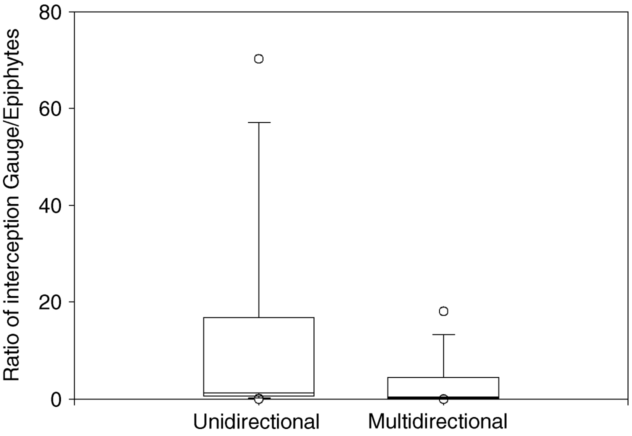

Figure 4. Distribution of the ratio of fog interception by two types of fog gauge relative to the amount collected by epiphyte samples after laboratory experiments. Mean ratio is significantly different from 1·0 for the unidirectional gauge ($P = 0{\cdot}01$) and suggestive of differences from 1·0 for the multidirectional gauge ($P = 0{\cdot}1$)

Fog interception and meteorological characteristics of fog events

Fog interception measured in the fog chamber was significantly related to both wind speed ($P < 0{\cdot}05$) and LWC ($P < 0{\cdot}01$) (Figure 6a and b). Fog interception peaked at a low-level wind speed (0·33 m s^{-1}) and at an intermediate LWC (106·7 mg m^{-3}) (Figure 6c). We were unable, however, to describe these relations using a mathematical response surface based on wind speed and LWC: in all cases, R^2 values were smaller than 0·30 ($P < 0{\cdot}05$).

Estimated values of LWC for our field experiments based on Equation (3) ranged between 10·3 and 69·5 mg m^{-3} s^{-1} and showed a significant relation with total interception measured by the multidirectional fog gauge (Figure 7; $R^2 = 0{\cdot}95$, $P = 0{\cdot}01$), as expected from the relation proposed by Tobón *et al.* (2006). Measurements of fog interception from our field experiments were related to the observations in the fog chamber, but were one to two orders of magnitude smaller ($P = 0{\cdot}07$). Notably, the values of LWC for our field observations were generally low compared with the range of values simulated in the fog chamber (Figure 8). On the other hand, wind speed ranged approximately over the same range as it did in our experiments in the fog chamber, although the lowest value in the field was higher than the lowest value registered in the fog chamber (Figure 8).

DISCUSSION

Relationship between actual fog interception by epiphytes and fog gauges

Our estimates of fog interception efficiency were significantly related to the uncorrected cloud water flux measured by the gauge for a wide range of interception values, as previously demonstrated by Frumau *et al.* (2006). However, for the multidirectional gauge, we found higher efficiencies in laboratory measurements relative to field measurements (Figure 3) and relative to the efficiencies

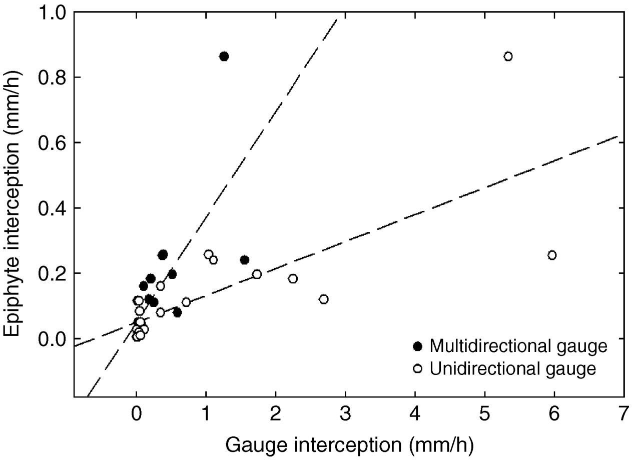

Figure 5. Regression analyses between fog interception by epiphytes measured in the fog chamber with interception measured by the multidirectional fog gauge (filled circles; $R^2 = 0{\cdot}53$, $P < 0{\cdot}01$) and by the unidirectional fog gauge (open circles; $R^2 = 0{\cdot}58$, $P < 0{\cdot}01$)

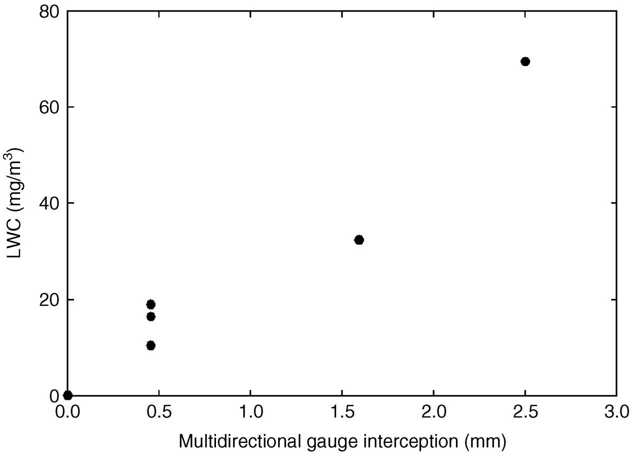

Figure 7. Calculated liquid water content (LWC) for fog events observed in the field based on fog interception by the multidirectional gauge (corrected for its efficiency) and wind speed

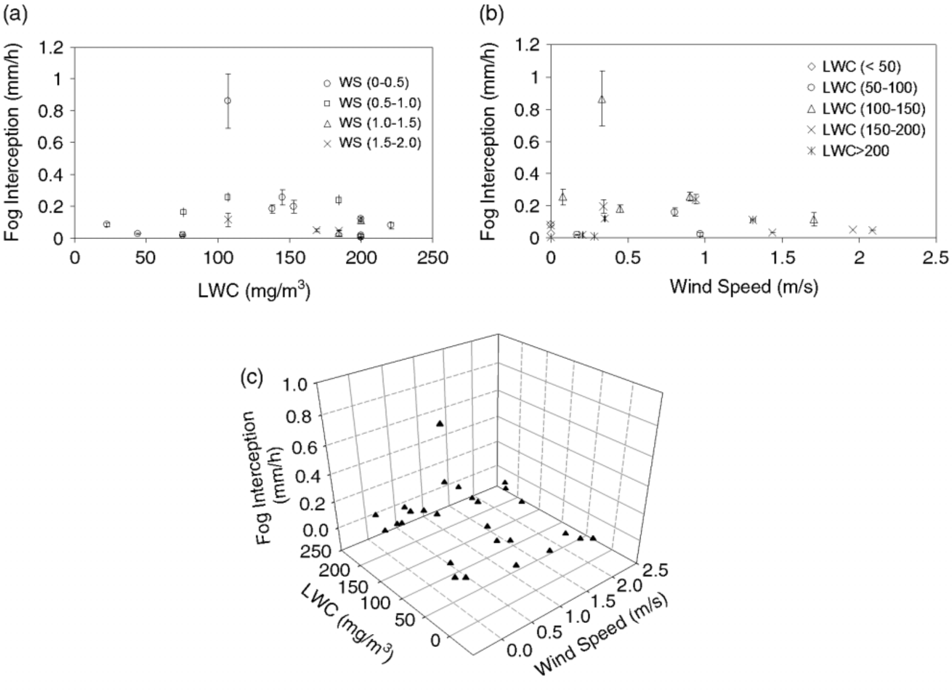

Figure 6. Relationship between fog water intercepted by epiphytes with (a) wind speed (WS), (b) liquid water content (LWC), and (c) both wind speed and LWC. Each point corresponds to the average fog interception (±1 SD, $n = 4$) by epiphytes for each fog event simulated on the laboratory

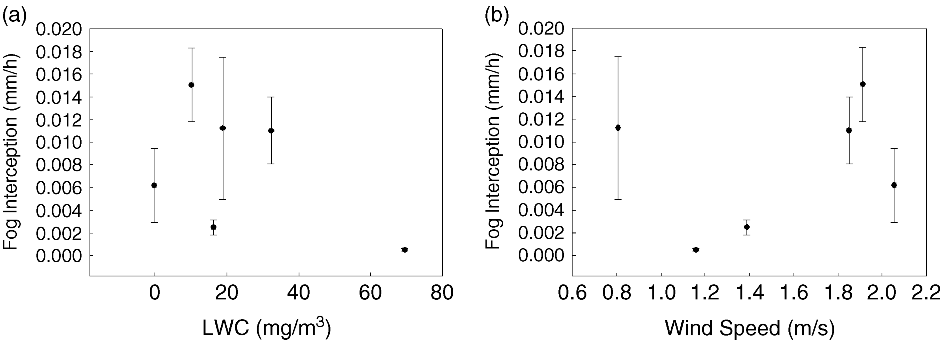

Figure 8. Relationship between fog water intercepted by epiphytes with (a) wind speed (WS) and (b) liquid water content (LWC) from observations in the field. Each point corresponds to the average (±1 SD, $n = 15$) fog interception by epiphyte samples exposed to natural fog events

reported by Frumau *et al.* (2006). These differences can be explained by the fact that our laboratory measurements were made under the controlled conditions of the fog chamber, where factors that contribute to the decrease in efficiency, such as enhanced evaporation occurring during periods of intermittent fog events, were not represented. As expected, interception efficiencies were higher on the multidirectional gauge than the unidirectional gauge. However, the multidirectional gauge in the field had efficiencies comparable to those of the unidirectional gauge in the fog chamber. In our experiments in the fog chamber, the unidirectional gauge was placed perpendicular to the almost constant fog-driving wind trajectory. This situation constitutes a simplification of the field conditions, where wind direction may vary during fog events. The variation of wind direction is an important factor that might decrease interception efficiency in these kinds of device.

Our results are consistent with others in indicating that fog gauges commonly used to measure fog interception in TMCFs can overestimate interception rates by epiphytes by approximately one order of magnitude (Bruijnzeel *et al.*, 2005). Our study builds on previous work to quantify those overestimations and highlights that the magnitude of such overestimations can be significantly reduced when the proper equations for interception efficiency are used. As suggested by Jarvis (2000), the epiphyte mass in TMCFs constitutes the most important source of fog interception in the forest, given the relatively large surface area and water-holding capacity associated with the epiphyte mass. Consequently, our estimated relationships between gauges and epiphytes are relevant at the ecosystem scale because the amount of fog interception by epiphytes is sufficiently large to influence forest hydrological fluxes, as suggested by previous research (Veneklaas *et al.*, 1990; Hölscher *et al.*, 2004).

Our results provide useful comparisons among gauge types, but we note that caution should be applied in extrapolating our comparison of the unidirectional gauge efficiencies in the fog chamber to the field because, as noted above, the unidirectional gauge was always oriented perpendicular to wind direction in the fog chamber. In the field, it is likely that the unidirectional gauge would often not be perpendicular to the main fog-carrying wind direction; therefore, fog interception efficiency would likely be smaller than that calculated here.

Fog interception and meteorological characteristics of fog events

Our results suggest that the fog interception is sensitive to the interaction between low levels of wind speed and intermediate values of LWC of fog, producing a synergistic response of high fog interception. These findings are consistent with previous theoretical descriptions of fog interception as a combined function of the turbulent flux of air through an intercepting surface, the amount of moisture of the moving air (LWC), the capacity of the vegetation to intercept water particles by deposition and impaction, and the area of vegetation exposed to the deposition and impaction fluxes (Merriam, 1973; Shuttleworth, 1977; Unsworth and Wilshaw, 1989; Bruijnzeel *et al.*, 2005). The fog chamber allowed us to manipulate some of these conditions and to test how interception varies along a wide range of potential combinations of wind speed and LWC. Some of those combinations might not occur frequently in the field, but they nonetheless provide important insights about fog interception processes over a broad range of potential field conditions.

Fog can be intercepted via two mechanisms: impaction and deposition. When the structural characteristics of vegetation are held constant, the predominance of each of these mechanisms depends upon the physical characteristics of the fog (LWC) and how it is transported across the intercepting surface. During periods of low wind speed, interception is driven primarily by deposition, especially for medium- to high-density fog events. However, at very high LWC levels, fog can settle by gravity, which is a different process than fog interception. On the other hand, as wind speed increases, impaction of fog onto vegetation might account for a greater proportion of fog interception. Theoretically, LWC is inversely related to wind speed (Equation (3)). As wind speed increases, LWC should decrease and the potential for evaporation of intercepted water should increase (because potential evaporation is proportional to wind speed; Shuttleworth, 1993), resulting in a reduction in net interception for a fog event (Figure 9).

Although fog interception might generally be expected to increase linearly with LWC due to a greater availability

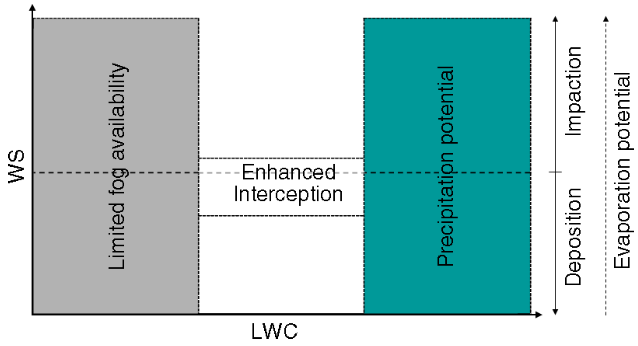

Figure 9. Hypothesized interactions between liquid water content (LWC) and wind speed (WS). Fog interception is hypothesized to be constrained at low LWC by limited fog availability and at high LWC by precipitation potential. At intermediate values of LWC, fog interception is hypothesized to be greatest at intermediate WS as a net result of the dependencies of deposition, impaction, and evaporation processes on WS

of moisture to be intercepted, this is not always the case. In a re-evaluation of data presented by Eugster *et al.* (2006) in a recent review of research on fog interception in TMCFs for studies that had measurements or estimations of LWC, we found that there was no significant linear relationship between LWC and fog interception ($R^2 = 0{\cdot}26$, $P = 0{\cdot}13$); rather, higher values of fog interception occurred at intermediate levels of LWC—values that are comparable to those for which we observed maximum interception. Although the results reported by Eugster *et al.* (2006) for fog interception do not include measurements of wind speed, our results suggest an explanation for the additional variance in the reported values.

Our laboratory experiments included ranges of meteorological conditions that were not observed during our experiments in the field and might represent extreme situations. Nonetheless, the amounts of fog intercepted by epiphytes that we measured were comparable to those reported for field conditions by previous studies (Chang *et al.*, 2002; Tobón *et al.*, 2006). Further, our results highlight potentially important interactions in meteorological conditions that drive maximal fog interception. Our results also highlight the need to evaluate interactions systematically among meteorological conditions in the field under a broader range of climatic conditions. Our findings are also constrained to fog interception by epiphytes themselves, which represent an important vegetation component of TMCFs but which alone do not mimic the overall structural complexity of a forest stand. Additional laboratory and field measurements are needed to understand the dynamics of fog interception by other types of vegetation structure in relation to meteorological characteristics.

Our field measurements of fog interception were considerably smaller than measurements in the fog chamber. Notably, the field measurements occurred under conditions that included intervals with high wind speeds, low LWC and higher radiation, all of which increase vapour pressure deficit in the atmosphere and, consequently, evaporation. This combination of conditions in the field apparently led to lower amounts of fog interception and could contribute to surface drying between sequential pulses of fog, as observed in our results.

Our results, which highlight the interaction between wind speed and LWC on fog interception, indirectly support the current consensus about the potential consequences of climate variation and change on TMCFs. Previous studies and assessments have noted that these ecosystems are particularly sensitive to increases in temperature that could result in the cloud belts rising above the elevation belts at which such forests are located, with further consequences on LWC and wind patterns (Still *et al.*, 1999). Our results suggest that even meteorological changes leading to modifications in LWC and wind speed, let alone temperature, can alter the potential amount of fog intercepted by epiphytes, thereby directly impacting important hydrological and ecological processes.

CONCLUSIONS AND SUMMARY

Estimates of fog interception obtained on epiphytes were correlated with those obtained from fog gauges but were more than an order of magnitude smaller, highlighting the importance of measurement approach when including gauge-based estimates of fog interception in the quantification of hydrological fluxes on TMCFs. Our laboratory results spanned a broad range of LWC for fog and indicate that fog interception is sensitive to an interaction between wind speed and LWC. Our results, considered in concert with results from other studies, lead us to hypothesize that fog interception is constrained at high and low values of LWC and that under intermediate LWC, fog interception increases with wind speed as a net result of deposition, impaction, and evaporation processes until interception begins to decrease with further increases in wind speed, due to potential changes in atmospheric water demand. An improved understanding of the sensitive interactions between fog interception and meteorological conditions is acutely needed to assess potential impacts of climate change on TMCFs and other fog-dependent ecosystems. Our findings provide a step in this direction and build on previous work to provide a revised hypothesis about the meteorological conditions driving fog interception rates that lead to additional understanding and predictive capability.

ACKNOWLEDGEMENTS

We thank the GIGA Research Group at the Universidad de Antioquia, Colombia, for financial support of this study. We also thank the Postgrado en Bosques y Conservación Ambiental and the Laboratorio de Ecología y Convervación Ambiental (LECA) at the Universidad Nacional de Colombia, Sede Medellín, for facilitating equipment and laboratory space. We thank CORANTIOQUIA for supporting the realization of this study on their property and for facilitating the weather station for both the laboratory and field experiments. This work was also supported by University of Arizona Agricultural Experiment Station Project See org.

REFERENCES

Adarve JC, Molina FJ. 1984. Evaluación preliminar de la circulación de vientos en el valle de Aburrá. *Revista Ainsa* **4**(1): 5–24.

Benzing DH. 1998. Vulnerabilities of tropical forests to climate change: the significance of resident epiphytes. *Climatic Change* **39**: 519–540.

Bruijnzeel LA. 2001. Hydrology of tropical montane cloud forests: a reassessment. *Land Use and Water Resources Reasearch* **1**: 1·1–1·18. http://www.luwrr.com/uploads/paper01-01.pdf [7 June 2006].

Bruijnzeel LA, Proctor J. 1995. Hydrology and biogeochemistry of tropical montane cloud forests: What do we really know? In *Tropical Montane Cloud Forests*, Hamilton LS, Juvik JO, Scatena FN (eds). *Ecological Studies* 110. Springer Verlag: New York; 38–78.

Bruijnzeel LA, Eugster W, Burkard R. 2005. Fog as a hydrologic input. In *Encyclopedia of Hydrological Sciences*, vol. 1, Anderson MG, McDonnell JJ (eds). Wiley: Chichester; 559–582.

Burges SSO, Dawson TE. 2004. The contribution of fog to water relations of *Sequoia sempervirens* (D. Don): foliar uptake and prevention of dehydration. *Plant, Cell and Environment* **27**: 1023–1034. DOI: 10·1111/j.1365–3040·2004·01207.x.

Cavelier J, Solis D, Jaramillo AM. 1996. Fog interception on montane forest across the central cordillera of Panamá. *Journal of Tropical Ecology* **5**: 309–322.

Chang SC, Lai IL, Wu JT. 2002. Estimation of fog deposition on epiphytic bryophytes in a subtropical montane forest ecosystem in northeastern Taiwan. *Atmospheric Research* **64**: 159–167.

Clark KL, Nadkarni NM, Schaeffer D, Gholz HL. 1998. Atmospheric deposition and net retention of ions by the canopy in a tropical montane forest, Monteverde, Costa Rica. *Journal of Tropical Ecology* **14**: 27–45.

Dawson TE. 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. *Oecologia* **117**: 476–485. DOI: 10·1007/S004420050683.

Eugster W, Burkad R, Holwerda F, Scatena FN, Bruijnzeel LA. 2006. Characteristics of fog and fogwater fluxes in a Puerto Rican elfin cloud forest. *Agricultural and Forest Meteorology* **139**: 288–306. DOI: 10·1016/j.agrformet.2006·07·008.

Foster P. 2001. The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Reviews* **55**: 73–106. DOI: 10·1016/S0012-8252(01)00 056-3.

Frahm JP. 1990. The ecology of epiphytic bryophytes on M. Kinabalu, Sabah (Malaysia). *Nova Hedwigia* **51**: 121–132.

Frumau KFA, Burkad R, Schmid S, Bruijnzeel LA, Tobon-Marin C, Calvo J. 2006. Fog gauge performance under fog and wind-driven rain conditions. In *Mountains in the Mist: Science for Conserving and Managing Tropical Montane Cloud Forests*, Bruijnzeel LA (ed.). University of Hawaii Press: Honolulu, HI (in press).

González J. 2000. Monitoring cloud interception in a tropical montane cloud forest of the south western Colombian Andes. *Advances in Environmental Monitoring and Modelling* **1**: 97–117. http://www.kcl.ac.uk/advances [6 July 2007].

Hafkenscheid RLLJ. 2000. *Hydrology and biogeochemistry of montane rain forests of contrasting stature in the Blue Mountains of Jamaica*. PhD thesis, Vrieje Universiteit, The Netherlands.

Hamilton L, Juvik JO, Scatena F (eds). 1995. *Tropical Montane Cloud Forests*. *Ecological Studies* 110. Springer Verlag: New York.

Hölscher D, Köhler L, van Dijk AIJM, Bruijnzeel LA. 2004. The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. *Journal of Hydrology* **292**: 308–322. DOI: 10·1016/j.hydrol.2004·01·015.

Holwerda F, Burkard R, Eugster W, Scatena FN, Meesters AGCA, Bruijnzeel LA. 2006. Estimating fog deposition at a Puerto Rican elfin cloud forest site: comparison of the water budget and eddy covariance methods. *Hydrological Processes* **20**: 2669–2692. DOI: 10·1002/hyp.6065.

Jarvis A. 2000. Measuring and modelling the impact of land-use change in tropical hillsides: the role of cloud interception to epiphytes. *Advances in Environmental Monitoring and Modelling* **1**: 118–148. http://www.ambiotek.com/advances/advemm/vol1no1/jarvis.pdf [6 July 2007].

Juvik JO, Ekern PC. 1978. *A climatology of mountain fog at Mauna Loa, Hawai'i Island*. Technical Report No. 118, Water Resources Research Center, Hawaii.

Juvik JO, Nullet D. 1995. Comments on 'A proposed standard fog collector for use in high elevation regions'. *Journal of Applied Meteorology* **34**: 2108–2110. DOI: 10·1175/1520-0450(1995)034<2108:COPSFC>2·0.CO;2.

Kerfoot O. 1968. Mist precipitation on vegetation. *Forestry Abstracts* **29**: 8–20.

Mejía O. 2002. *Un modelo estacionario de circulación diurna en el valle de Aburrá para época de verano*. MSc thesis. Universidad de Antioquia, Colombia.

Merriam RA. 1973. Fog drip from artificial leaves in a fog wind tunnel. *Water Resources Research* **9**: 1591–1598.

Mulligan M, Burke SM. 2005. *DFID FRP Project ZF0216 Global cloud forests and environmental change in a hydrological context*. Final report, December.

Nieder J, Prosperí J, Michaloud G. 2001. Epiphytes and their contribution to canopy diversity. *Plant Ecology* **153**: 51–63.

Richardson BA, Richardson MJ, Scatena FN, McDowell WH. 2000. Effects of nutrient availability and other elevational changes on bromeliad populations and their invertebrate communities in a humid tropical forest in Puerto Rico. *Journal of Tropical Ecology* **16**: 167–188. DOI: 10·1017/S0266467400001346.

Schemenauer RS, Cereceda P. 1994. A proposed standard fog collector for use in high elevation regions. *Journal of Applied Meteorology* **33**: 1313–1322. DOI: 10·1175/1520-0450(1994)033<1313: APSFCF>2·0.CO.

Shutttleworth WJ. 1977. The exchange of wind-driven fog and mist between vegetation and the atmosphere. *Boundary-Layer Meteorology* **12**: 463–489.

Shuttleworth WJ. 1993. Evaporation. In *Handbook of Hydrology*, Maidment DR (ed.). McGraw Hill: New York; 4·1–4·53.

Spraying Systems Co. 1997. *Performance data for No. 23 412-1/4- & No. QJ25655 Airjet® Fogger Nozzles (metric)*. Data sheet no. 23 412-2M.

Still CJ, Foster PN, Schneider SH. 1999. Simulating the effects of climate change on tropical montane cloud forests. *Nature* **398**: 608–610. DOI: 10·1038/19 293.

Tobón C, Köhler L, Bruijnzeel LA, Frumau KFA, Schmid S. 2006. Water dynamics of epiphytic vegetation in a lower montane cloud forest: Fog interception, storage and its evaporation. *Conference Proceedings Mountains in the Mist: Science for Conserving and Managing Tropical Montane Cloud Forests. 2nd International Symposium on Tropical Montane Cloud Forests*, Waimea, Hawaii, 27 July–1 August 2004.

Unsworth MH, Wilshaw JC. 1989. Wet, occult and dry deposition of pollutants on forests. *Agricultural and Forest Meteorology* **47**: 221–238. DOI: 10·1016/0168-1923(89)90 097-X.

Veneklaas EJ, Zagt EL, Van Leerdam A, Van Ek R, Broekhoven AJ, Van Genderen M. 1990. Hydrological properties of epiphyte mass of a montane tropical rain forest. *Vegetatio* **89**: 183–192. DOI: 10·1007/BF00032170.

Warton DI, Wright IJ, Falser DS, Westoby M. 2006. Bivariate line-fitting methods for allometry. *Biological Reviews of the Cambridge Philosophical Society* **81**: 259–291. DOI: 10·1017/S1464793106007007.

Wolf JHD. 1996. *Ecology of epiphytes and epiphyte communities in montane rainforest*, Colombia. Hugo de Vries Laboratory Special Publication, Amsterdam.