

Fog interception by Ball moss (*Tillandsia recurvata*)

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Abstract. Interception losses are a major influence in the water yield of vegetated areas. For most storms, rain interception results in less water reaching the ground. However, fog interception can increase the overall water storage capacity of the vegetation and once the storage is exceeded, fog drip is a common hydrological input. Fog interception is disregarded in water budgets of semiarid regions, but for some plant communities, it could be a mechanism offsetting evaporation losses. *Tillandsia recurvata* is a cosmopolitan epiphyte adapted to arid habitats where fog may be an important water source. Therefore, the interception storage capacity by *T. recurvata* was measured in controlled conditions and applying simulated rain or fog. Juvenile, vegetative specimens were used to determine the potential upperbound storage capacities. The storage capacity was proportional to dry weight mass. Interception storage capacity (C_{\min}) was 0.19 and 0.56 mm for rainfall and fog respectively. The coefficients obtained in the laboratory were used together with biomass measurements for *T. recurvata* in a xeric scrub to calculate the depth of water intercepted by rain. *T. recurvata* contributed 20% to the rain interception capacity of their shrub hosts: *Acacia farnesiana* and *Prosopis laevigata* and; also potentially intercepted 4.8% of the annual rainfall. Nocturnal stomatic opening in *T. recurvata* is not only relevant for CO₂ but for water vapor, as suggested by the higher weight change of specimens wetted with fog for 1 h at dark in comparison to those wetted during daylight (543 ± 77 vs. 325 ± 56 mg, $p = 0.048$). The storage capacity of *T. recurvata* leaf surfaces could increase the amount of water available for evaporation, but as this species colonise montane forests, the effect could be negative on water recharge, because potential storage capacity is very high, in the laboratory experiments it took up to 12 h at a rate of 0.261 h^{-1} to reach saturation conditions when fog was applied.

1 Introduction

Atmospheric bromeliads have developed the ability to survive in environments where the rain period is limited. Also, throughout the dry season they show asynchrony in the leaf phenology compared to the rest of the community, owing to distinctive anatomical and physiological traits (Barradas and Glez-Medellin, 1999). Their crassulacean acid metabolism (CAM), is characterized by the stomatic absorption of CO₂ during darkness, as well as restricted water lost from transpiration (Nobel, 1983). Regarding bromeliads, leaf water is coupled to the atmospheric water vapor, but the degree of coupling depends on life form, microclimate and vertical strata within the canopy (Reyes-García et al., 2008b). The bromeliads absorb water through specialized structures such as foliar trichomes and stomata, when the level of atmospheric water is high or during periods of nocturnal fog (Benzing, 2000; Reyes-García et al., 2008b). Atmospheric species of bromeliad colonize the tree canopy, rocks and even cable lines and therefore, the only water available to them is that detained on their surfaces and the atmospheric vapor available in the limit layer. The role of trichomes is very important for water detention; when the humidity content in the plant is low, the trichome wings are elevated and when moist, they are folded and stick to the leaf surface (Schmitt et al., 1989; Stefano et al., 2008). When the trichomes' wings are folded a reduction in the contact angle with rain or fog drops is possible and the runoff from the surface could be decreased. Although the atmospheric bromeliads do not have roots to absorb water or a tank to capture rainfall, the number of narrow leaves are enough to capture the fog and help satisfy their water requirements (Martorell and Ezcurra, 2007). Reyes-García et al. (2008a) suggested that dew and fog interception are important mechanisms because the main photosynthetic activity of atmospheric bromeliads is during the rainless time of the year.



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On the other hand, hydrological understanding has advanced substantially during recent decades, particularly regarding the natural evaporation process (Shuttleworth, 2007). A main component of evaporation is rainfall interception loss generated from the vegetation canopy (Dunkerley, 2000). Measurement of rainfall interception has been investigated in temperate and tropical forests, but studies in semiarid shrubland or grasslands are scarce (Crockford and Richardson, 2000). Nevertheless, N avar and Bryan (1990, 1994) and N avar et al. (1999) showed that interception losses in a thorny scrub could exceed 27% of the annual precipitation. For dry climates, the magnitude of interception is important with respect to the annual rainfall, the shortage of water resources and the temperature increases due to global warming (M endez et al., 2008).

As with rain, fog interception research mainly describes tropical and temperate forests. In the Tropical Montane Cloud Forests fog interception contributes up to 154% of annual rainfall and, is an important process during the dry season (Bruijnzeel, 2001, 2005). The interception capacity of epiphytes is high but only a fraction of the potential storage could be actually available, because the mosses are usually close to saturation or most of the moss biomass occurs at sheltered positions in the lower part of the canopy (H olscher et al., 2004).

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 (Villegas et al., 2008). By monitoring changes in their biomass, the epiphytes are used as biosensors to better quantify the magnitude and mechanisms of fog interception (Mulligan et al., 2011). For dry climates these measurements are more important because the small amounts of atmospheric water, fog or dew are paramount for the biotic diversity (Brown et al., 2008). The availability of water in dry climates is not abundant, but probably is sufficient to establish an independence from the soils' water relations; as in the case of epiphytic bromeliads (Reyes-Garc a et al., 2008b).

Maximum water content of epiphytes has been assessed by submerging samples in water or applying simulated rain (Pypker et al., 2006). Also, there is a discrepancy in specific storage measured by dipping vegetation into water compared to sprinkling experiments, especially when water is blotted from foliage to simulate windy conditions; storage measured this way is nearly an order of magnitude lower than under rainfall simulation (Keim, 2006).

Interception loss is the amount of rainfall detained and subsequently evaporated from the vegetation, the boundary layer conductance and canopy storage capacity are the most important parameters in all models of rainfall interception loss by forest canopies. Rutter et al. (1971) defined the storage capacity as the depth of water which can be stored or detained on the plant surfaces in still air. Canopy storage is added to by intercepted rainfall and depleted by evaporation and drainage (Rutter et al., 1971). Two primary methods to

estimate interception losses are: (i) calibrated process-based models of interception and evaporative loss and (ii) direct measurement (Dunkerley, 2000). The measurements of interception presents some problems because storage is modified by intensity of rainfall, wind speed and direction (Crockford and Richardson, 2000). In the case of fog, Villegas et al. (2008) showed that interception rates by Ball moss (*Tillandsia recurvata*) were sensitive to the interaction between low levels of wind speed and liquid water content of fog. The interaction between wind speed and fog interception rate results from vertical settlement at low speeds and advective impactation at high speeds.

The storage capacity parameters are better identified when evaporation is low (Vrugt et al., 2003). Since radiation is low during rainfall, the evaporation rate during storms is predominantly determined by the aerodynamic conductance (Rutter et al., 1971). Including only storms under zero evaporation conditions will yield a value which is a better estimate of the canopy storage than considering storms with non-zero evaporation (Gash, 1979). Storage parameters are calculated using measurements of the weight gained by a specimen that is exposed to simulated rain, preferably in still air and for saturated surfaces (Dunkerley, 2000).

Interception losses are related to precipitation characteristics, evaporation rate and the amount of water stored on vegetation surfaces (C). Two parameters of interception storage are important: maximum storage (C_{\max}), which is the water stored when drainage rate is constant, C_{\max} includes water temporarily stored and that would be removed by gravity and; residual or minimum storage (C_{\min}), that depth of water removed only by evaporation (Pitman, 1989; Putuhenana and Cordery, 1996). The value of C_{\min} is equivalent to soil field capacity and also corresponds to the minimum quantity of water required to wet all the canopy surfaces (Rutter et al., 1971).

In the present work, we used direct methods to measure interception storage parameters of *T. recurvata* in laboratory experiments. Its objectives were to: (i) determine the storage capacity during daylight using three wetting methods: simulated rain, simulated fog and soaking; (ii) simulate a short duration fog event during daylight and follow the weight loss for 12 h; (iii) assess the effect of daylight or dark conditions on the storage capacity of Ball moss and on weight loss after seven days post-event. The objectives would answer what is the potential storage with different wetting methods; how much water would be available at evening after an early morning fog event and; weather or not stomata opening is important in the water relations of Ball moss.

This study would improve our knowledge on water balance and ecology of semiarid shrublands because the aerial epiphyte communities, which grow in association with tree structures enhance interception of fog and rainfall (Villegas et al., 2008). Also, Bromeliad species as such as *T. recurvata* not only compete for space and light, but intercepted precipitation could have an influence on the amount of available

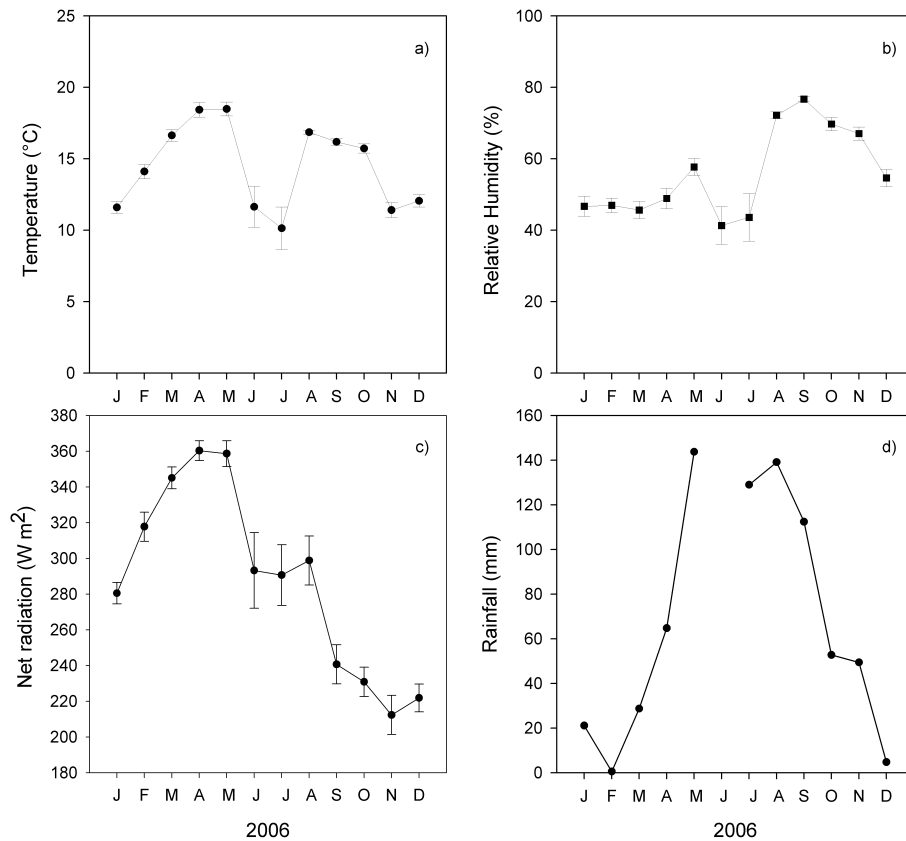


Fig. 1. Monthly means and standard errors for 24 h records of: (a) air temperature (T), (b) relative humidity (RH), (c) net radiation and, (d) rainfall at the study sites.

water and under severe invasion the growth of host species may be reduced.

2 Material and methods

2.1 Sites

The sites from which the data were taken, located in the Central Highlands of México are described as thorny scrub with *Prosopis laevigata* and *Acacia farnesiana* as dominant shrub species, both being phorophytes of *T. recurvata*. The altitude varies from 1959 to 1990 m a.s.l. (above sea level). The study area is classified in the Koeppen's Climate system as BS₁k.

During 2006, meteorological stations located at 20°43' N, 99°47' W (site A) and 21°13' N, 100°47' W (site B), measured rainfall, temperature (T), relative humidity (RH) and wind speed using a WXT510 multi-sensor (Vaisala, Helsinki, Finland). Net radiation was measured with a Q7.1 net radiometer (Campbell Scientific Ltd., Shepshed UK). These sensors were connected to a CR1000 datalogger (Campbell Scientific Ltd., Shepshed UK), averaging at a 1 min time step.

The average annual T and RH prevailing at the study sites were 14.9 °C and 51.7 %. Figure 1 presents monthly means

for 24 h for T and RH, rainfall and net radiation. During the early hours of the morning (04:00 a.m. to 08:00 a.m.), T and RH were 11.1 °C and 79.7 %; from 08:00 a.m. to 04:00 p.m., after the potential fog period, values were 21.4 °C and 36.1 %. Mean wind speed was 0.68 m s⁻¹ and net radiation was -32 W m⁻² during the early hours.

Dew point temperature was calculated using the Magnus-Tetens formula; the coefficients used were according to Murray (1967). Biomass annual production of *T. recurvata* reported by Olalde and Aguilera (1998) at site B was used to scale up laboratory measurements. Plant material used in the experiments was collected from a site close to the laboratory facilities (20°43' N, 100°24' W).

2.2 Plant material

Juvenile, vegetative specimens of *T. recurvata* were chosen because the trichomes of some bromeliads are reduced in frequency and dimension as the plant reaches the adult form (Stefano et al., 2008). This kind of specimens would represent the upper bound of water storage. Specimens were collected during the dry season, at morning hours and on the programmed day's experiment.

The plants used in the experiments were collected from the field at random but considering that the fresh mass of the specimen was within an established confidence interval. The fresh mass of 30 plants was measured and a 99% confidence interval was constructed ($\bar{x} \pm s_{\bar{x}} t_{\alpha/2=0.005, gl=29}$ where: \bar{x} is the fresh mass mean, $s_{\bar{x}}$ is the standard error of the mean and t the corresponding Student's t -distribution value for a 99% confidence and 29 degrees of freedom).

2.3 Storage capacity: simulated fog

The storage capacity of *T. recurvata* was directly determined in a laboratory where conditions of T and RH were stable, similar to those present in the study sites A and B during daylight (21.4 °C and 36.1 %). The plant was suspended by a 0.12 mm nylon line hooked to an electronic balance. A copper wire forming a hook at the end of line secured the specimen. The mass of the line and hook was 24 mg. The plant mass (W) was measured in 5 mg steps to the nearest 1 mg. Data were acquired via the RS232 microcomputer port and using Bytewedge Pro version 3.3 (Fog software, Inc.). To control the fog spray a 50 × 55 cm bell-shaped polystyrene chamber was used (Fig. 2). The scale was located in a platform above the chamber and a 3 mm opening in the top of the chamber allowed movement of the line without obstruction. The chamber was placed on a metal base with several connection openings and a fog spray vent. Fog was produced by an ultrasonic humidifier at a rate of 0.261 h⁻¹ and 0.0004 mm mean drop size (Elelum 002, Sunshine, EM, México). A timer switched on and off the humidifier as required. Inside the chamber a Hobo Pro sensor (Onset Corp., Bourne, MA) recorded T and RH every 5 min. A *petri* dish with water was placed inside the chamber to satisfy evaporative demand during the draining phase of the experiment. Pypker et al. (2006) in their experiments of rainfall interception by epiphytes used a similar conditions (high RH and 22 °C temperature).

Ten plants were individually wetted by simulated fog during 12 h. Constant weight was reached during the last 3 h. After the wetting period ended another 12 h were allowed for the draining phase. Maximum storage capacity was calculated as:

$$C_{\max} = Wf_{\max} - Wf_0. \quad (1)$$

where Wf_0 [mg] was the plant mass before the wetting phase and Wf_{\max} [mg] was the plant mass at saturation. The minimum storage capacity was calculated as:

$$C_{\min} = Wf_{\min} - Wf_0. \quad (2)$$

where Wf_{\min} [mg] was the plant mass at the end of the draining phase and assuming that evaporation was negligible. At the end of each run the plant dry weight (W_s) was obtained by oven-drying at 60 °C for 48 h. Water content was determined as:

$$H = Wf_0 - W_s. \quad (3)$$

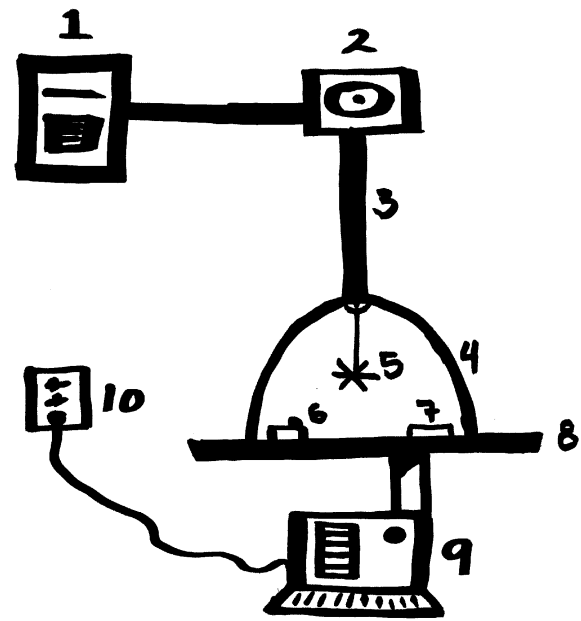


Fig. 2. Diagram of the fog simulation setup (1) computer, (2) electronic scale, (3) nylon line, (4) chamber, (5) *Tillandsia recurvata* sample, (6) humidity and temperature sensor, (7) petri dish, (8) metallic base, (9) humidifier, (10) timer.

2.4 Storage capacity: simulated rain

Ball moss within shrub canopies is mainly found at the mid and lower branches (García-Suárez et al., 2003) and therefore, throughfall interception may be more important than rainfall interception. Drop size distribution of secondary drops ranges from 0.5 to 5.5 mm and is characteristic of particular tree species (Calder et al., 1996). Throughfall had different drop size distribution among canopy species under conditions of little canopy vibration with low rainfall intensity and wind speed; but throughfall contained smaller drops under conditions when rainfall intensity was high (Nanko et al., 2006). Convective high intensity rainfall is typical in the region; therefore, small, low velocity drops were used.

Thirty specimens were used to estimate the mean minimum interception storage capacity by rain. Spray was horizontally applied over the specimen to produce low velocity drops, representing throughfall within the tree canopy that could be intercepted by epiphyte vegetation. Two manual sprayers were operated at a constant time rate. Rainfall was measured with a TE-525LL-L tipping bucket (Texas Electronics Inc., Dallas TX) calibrated to record 0.254 mm per tip. Rainfall intensity was 70 to 79 mm h⁻¹ and drop diameter was 1.8 ± 0.2 mm. The simulation stopped when the weight of the wetted specimen was constant. The drying phase was 12 h or until drainage finished.

2.5 Storage capacity: soaking

Some authors have reported the maximum water holding capacity (S) as the amount of water detained by a material after soaking for a period of time and a draining phase (Sato et al., 2004; Pypker et al., 2006). For *T. recurvata* it would be expected that any air trapped in the surface irregularities was eliminated and then S could be different from C_{\max} or C_{\min} . Conceptually, S would be similar to C_{\min} if the wetted surface was smooth, because both represent water storage after saturation and draining. However, water fluxes must be different for rough surfaces when wetted by soaking, rain or fog.

A sample of ten plants was used. Values of S were determined by measuring Wf_0 and then suspending the plant as previously described. A 500 ml container was placed below the specimen and filled using a venoclysis and a syringe until the plant was immersed. The container was emptied by gravity after 3 h and the plant immediately weighed to assess Wf_{\max} . The mass after 12 h of draining represented Wf_{\min} , assuming that evaporation was negligible. Values of S were determined as:

$$S = Wf_{\min} - Wf_0. \quad (4)$$

2.6 Short duration fog event

The experiments described were designed to estimate the values of C_{\max} , C_{\min} and S . However, field conditions in the thorny scrub are adequate for fog formation only during few hours of the day and, not every day (García-García and Zarraluqui, 2008). In this experiment the evolution of C was followed during 1 h of wetting with simulated fog and 12 h drying phase. The C determined at the end of the experiment would represent the available water on the specimen surface at the early night when stomata could open. Any water available for evaporation at the plant surface would reduce evaporative demand because stomatal control of transpiration is strong only when boundary layer conductance is high in relation to stomatal conductance. Also, if no water was left after 12 h, then water absorption through stomata or trichomes could only take place during the simulated fog event.

Twelve plants were randomly assigned to two treatments: control and wetted with fog during daylight. Afterwards, the change in fresh mass (ΔWf) was recorded for seven days for all plants. Plants were placed in the laboratory where T was 22 °C and RH was $\leq 30\%$; these were similar to field conditions from 08:00 a.m. to 04:00 p.m.

2.7 Day and night fog events

All the tests described were performed during daylight. However, the values of C and S correspond to live specimens of *T. recurvata* and it was impossible to partition the water stored on the plant surfaces from that probably absorbed via stomata and trichomes during the wetting phase.

During the day, stomata would be closed and therefore, plant mass should be lower than that of plants wetted at dark. We assumed that foliar trichomes absorb fog water and are functional following light or RH daily cycles. Schmitt et al. (1989) determined that bromeliad may take up water from the gas phase of the atmosphere, when the RH increases, by equilibration of the hygroscopic cell walls of the dead scale cells in the trichomes. These authors concluded that this gain in water is lost when RH decreases at the beginning of the following day, so bromeliad do not have a net gain of water from this mechanism. To cast some light on this aspect, six specimens were fog wetted from 05:00 to 06:00 a.m. at dark; another six were wetted during daylight, but at the same time schedule. ΔWf was recorded during the following seven days.

2.8 Interception scaling up

Potential storage capacities of *T. recurvata* in the vegetation were calculated as a function of Wf_0 (Pitman, 1989):

$$C' = \frac{C}{Wf_0}. \quad (5)$$

$$S' = \frac{S}{Wf_0}. \quad (6)$$

where C'_{\max} , C'_{\min} and S' have units mg mg^{-1} . Afterwards, mean values were multiplied by the biomass reported by Olalde and Aguilera (1998) to obtain the intercepted depth of water [mm].

Based on the rain wetting experiment, the estimation of annual interception was the result of the number of rain events greater than 0.19 mm multiplied by the storage capacity, 0.19 mm. Rain events smaller or equal to 0.19 mm were added up. Rainfall events were identified as storms separated by periods of time longer than 24 h.

2.9 Statistical analysis

The relationship between storage capacity and biomass was explored by regression analysis and using Table Curve 2-D v 5.01 (Sistat Software Inc.). ANOVA and the Tukey test were performed to estimate the difference among S and C values. A repeated measures model was used to assess differences regarding ΔWf over time. The level of significance was fixed at $\alpha = 0.05$. All tests were performed using the GLM and MIXED procedures of SAS (SAS Institute, Cary, NC, USA).

3 Results and discussion

3.1 Storage capacity

Three wetting methods were applied to determine the water storage capacity of Ball moss and, there were differences

Table 1. Interception storage capacity of *T. recurvata* in laboratory conditions.

	Soaking Mean	SE*	Fog Mean	SE*	Rain Mean	SE*
mg						
Wf_0^1	1953	297	1453	116	2110	191
W_S^2	709	29	482	126	873	92
S^3	1783	353				
C_{max}^4			2788	484		
C_{min}^4			1610	329	942	444
mg mg ⁻¹						
S'^5	0.89	0.09				
C'_{max}^5			2.04	0.26		
C'_{min}^5			1.41	0.19	0.47	0.02
mm						
S	0.36					
C_{max}^4			0.81			
C_{min}^4			0.56		0.19	

¹: fresh weight, ²: dry weight, ³: maximum storage capacity, ⁴: the maximum and minimum interception storage capacities, ⁵: the capacities per unit of fresh mass, *: standard error of the mean.

between the methods for the amount of water stored after a draining phase was allowed. Soaking the specimen was not representative of rainfall or fog events because the storage parameter S' was different from C'_{min} under simulated fog or rain ($p = 0.03$); therefore, the soaking method would not be advisable for water relations studies of species like *T. recurvata*. Table 1 presents the storage coefficients obtained in the laboratory.

Leaf and trichomes traits could explain the difference between values of C'_{min} in relation to S' . Sato et al. (2004) reported similar S for leaf litter of species with trichomes or glabrous, but C_{min} values were higher for the species with trichomes, they suggested that drop size and aggregation are important for storage capacity and drainage. In the present work, it was possible that coalescence increased drainage in the immersion tests for S' but this phenomena probably was not as important as in the case of fog simulations, due to the smaller drop diameter; thus, C'_{min} was also higher for fog compared to rain ($p \leq 0.0001$). Although the dominant forces contributing to water storage are gravity and capillary adsorption-tension, viscous forces also are an important component in water retention, as in the case of surfaces where the flux is slow and with a high roughness coefficient. Contact angle is an indicator of water repellency of a surface and this trait has great ecological importance. Droplet contact angle and droplet retention are inversely proportional to the trichome density (Pandey and Nagar, 2003). In the case

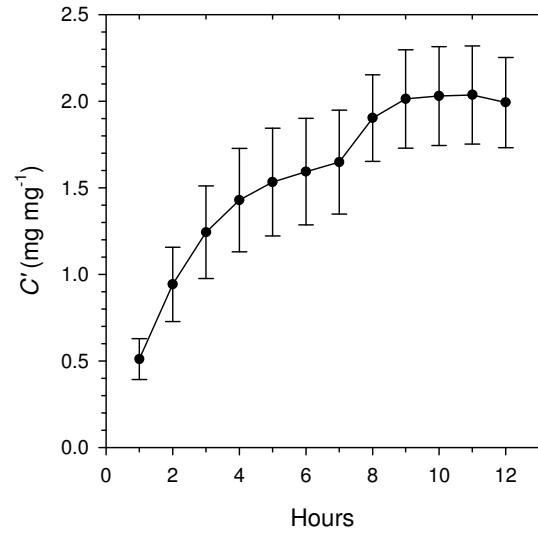


Fig. 3. Means and standard error of stored water in *T. recurvata* during 12 h wetting by simulated fog at $\geq 90\%$ RH and 22 °C.

of *T. recurvata* trichome wings movement during the wetting phase also would have to be considered to explain drainage fluxes and storage capacities.

According to these results, water was better captured by *T. recurvata* when fog forms. However, natural fog rate in the study site probably was much smaller than the flows generated during the experiments, mainly because fog events are shorter in duration than the 12 h period used in the experiment. Fog events could last less than three hours in the study sites according to the temperature records. For example, stored fog during the first hour of simulation was 50 % of Wf_0 and by the third hour it was 120 % (Fig. 3).

Jarvis (2000) reported the storage capacity of epiphytics after 30 h of fog simulation at 6.41h^{-1} as 5.94 times their dry weight whereas in the present work it was 4.53 times after 12 h at 0.261h^{-1} . Applying a lower rate, similar to those reported in nature, would result in longer test runs. More importantly, the result suggest that for *T. recurvata*, fog interception could not be a transfer mechanism, through drainage, beneficial to terrestrial species and therefore, the ecological relevance of fog interception by *T. recurvata* probably is indirect, if any.

Finding an allometric relationship for the storage parameters is important to scale up the storage capacities. Leaf area or number of leaves are cumbersome to measure, but total biomass was an easily measurable trait of *T. recurvata* and in the fog simulation tests Wf_0 was related to C_{max} and C_{min} ($C_{max} = -728.77 + 2.11 Wf_0$, $r^2 = 0.52$, $p = 0.02$; $C_{min} = -790.91 + 3.14 Wf_0$, $r^2 = 0.56$, $p = 0.02$). In the case of simulated rain the relationship was $C_{min} = 129.34 + 0.38 Wf_0$, $r^2 = 0.79$, $p \leq 0.0001$. For these relations the explained variance by Wf_0 was low. The relationship could improve increasing the number of samples

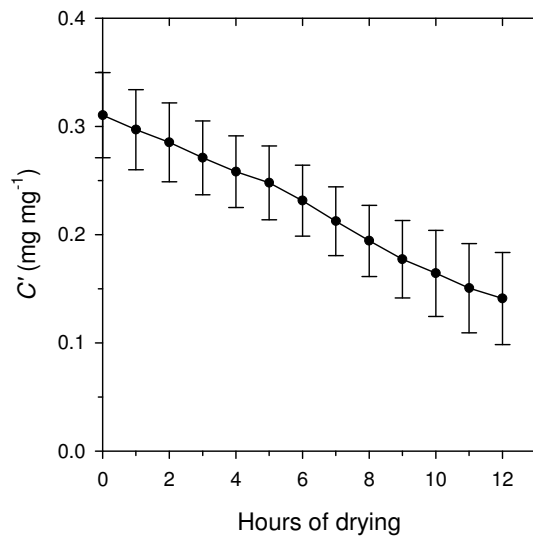


Fig. 4. Means and standard error of stored water in *T. recurvata* after 1 h wetting by simulated fog at $\leq 30\%$ RH and 22°C .

or including other other traits, such as number of leaves or density of trichomes (Martorell and Ezcurra, 2007). Biomass dry weight (W_s) was not related to C_{\max} or C_{\min} because the plant water content was variable, despite the relatively constant ambient during the dry season and phenological development of the specimens.

3.2 Short duration fog event

There was no statistical difference in the daily weight change rate during one week of drying between plants fog wetted for 1 h ($-29.4 \pm 6.6 \text{ mg d}^{-1}$) and those not wetted ($-15.5 \pm 6.0 \text{ mg d}^{-1}$). Fifty percent of the intercepted water, during 1 h of fog wetting, was lost after 12 h of drying at low RH (Fig. 4). Because the wetting occurred during daylight there was little opportunity for water to be absorbed through stomata and probably very little of the water remaining on the plant surfaces after 12 h was useful for the plant. The stored water inside the plant before the experiment was the most likely source of water for the observed change in weight.

3.3 Day and night fog events

Specimens wetted for 1 h at dark gained more weight in comparison to wetting during daylight (C , Table 2). However, both treatments stored a similar amount of water per unit of fresh mass (C' , 0.215 vs. 0.201 mg mg^{-1}) immediately after the fog simulation ended. At this point during the experiment both treatments had a similar amount of water “stored” but probably the partition was different.

Specimens wetted at dark lost less weight after seven days of drying following the fog simulation. This result was interpreted as higher water detention inside the plant as a

Table 2. Weight and storage of *T. recurvata* after a one hour fog event at daylight or dark in laboratory conditions.

		Daylight Mean	SE*	Dark Mean	SE*	Sig.**
Wf_0^1	mg	1677	256	2908	541	n.s.***
C^2	mg	325	56	542	77	0.05
ΔWf^3	mg	-244	78	-28	63	0.03
C^2	mg mg^{-1}	0.215	0.04	0.201	0.03	n.s.
ΔWf^3	mg mg^{-1}	-0.134	0.04	-0.001	0.02	0.01

¹: fresh biomass, ²: storage, ³: the change in fresh mass, *: standard error of the mean, **: Significance, ***: not significant at the 0.05 level.

consequence of nocturnal stomatic opening during CO_2 assimilation since *T. recurvata* is a CAM species. Proportional to the initial fresh weight, the weight loss represented -1% and -15% , for dark and light conditions respectively.

These results showed that *T. recurvata* water relations depended upon recurrent conditions favorable for fog formation or condensation. The experiment at dark also suggested that stomata opening is more important than foliar trichomes regarding water relations. Schmitt et al. (1989) showed that the patterns of water uptake and loss are similar in dead or alive *T. recurvata* during day-night cycles with respectively low and high RH. In studies of leaf water isotopic enrichment Reyes-García et al. (2008b) also demonstrated the importance of water vapour exchanges at high humidity for epiphytic bromeliads. In our experiment ambient RH was low, temperature constant and water condensation was not possible; therefore, the plants could not gain weight from ambient water during the seven day drying phase.

3.4 Extrapolation to natural condition

Annual rainfall during 2006 was 732 and 770 mm at sites A and B. González-Sosa et al. (2009) reported 30 and 20% rainfall interception by the canopy of *A. farnesiana* and 27 and 21% by *P. laevigata*. Standing biomass of *T. recurvata* was $4000 \pm 480 \text{ kg ha}^{-1}$ (Olalde and Aguilera, 1998). Scaled up C_{\min} for rainfall was 0.19 mm for *T. recurvata* (Table 1) and, 0.93 mm for the host shrubs *A. farnesiana* and *P. laevigata* (Mastachi, 2007).

We derived the annual interception of *T. recurvata* as 4.8% (35.8 mm) of annual rainfall. The biomass used in the calculation was important, as the site was considered infested by Ball moss, also juvenile specimens are more likely to intercept a higher amount of rainfall. Five percent interception loss represented the high bound figure and, still it was relatively small amount in terms of annual rainfall at the sites.

In terms of fog, 57 min were needed to intercept the same amount as the storage capacity for rain (0.19 mm). This value was obtained scaling up to area basis the data presented in Fig. 3 and using the relationship $C = -0.83 + 0.25 \ln(t)$,

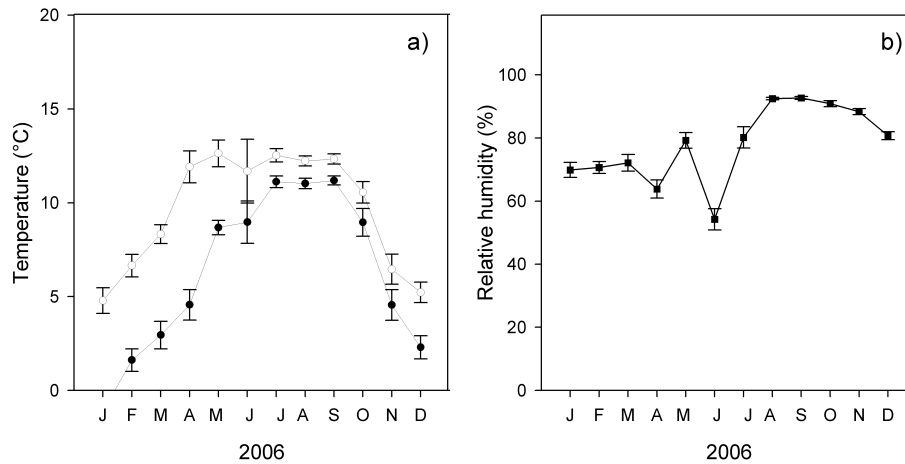


Fig. 5. Mean and standar error of (a) air temperature (○), dew point temperature (●) and (b) relative humidity (RH) for morning hours 04:00 to 08:00 a.m. at the study sites.

$r^2 = 0.98$, $p \leq 0.0001$; where t was time [min] and C was the stored water [mm].

The relative importance of fog relative to rainfall interception in field conditions needs to be investigated. Using Ball moss as real time biomonitor would be the best option, because fog gauges produce an overestimate (Villegas et al., 2008). Our results showed that Ball moss has a high monitoring capacity, as represented by the storage capacities and; good resolution over time, as showed by the dark experiments and the weight loss follow ups. An apparatus similar to that presented by Mulligan et al. (2011) for mosses could be designed for such monitoring with Ball moss.

Interpretation of the present data depends on the real fog amount and adequate conditions for vapor condensation in the air surrounding the shrub vegetation. Fog happens when the temperature and dew point are equal or within a degree (Gultepe et al., 2007), but during the rainy season the difference between T and T_r was 1.1 to 1.9 °C from July to November at 04:00 a.m. to 08:00 a.m. (Fig. 5). However, it should be considered that bromeliad leaf temperature is lower than air temperature at dawn (Andrade, 2003), thus condensation over surfaces could occur in absence of visible fog. Another factor important in fog formation is the evaporation from soil moisture and dew when the surfaces heat up (Gultepe et al., 2007). Higher T and T_r suggested that rainfall could be more important than fog for Ball moss water relations at the selected sites. Accordingly, Andrade (2003) concluded that dew deposition was not adequate to support growth for epiphytic bromeliads during the driest months of the year in a tropical dry forest. On the other hand, Martorell and Ezcurra (2002) identified fog belts at intermediate altitudes as a main determinant of species distribution and diversity in the rosette scrub in arid mountains (including bromeliads), altitude and temperature being of lesser importance. In either case, fog biomonitoring would be desirable, and growth should independently measured.

3.5 Considerations and implications

Drop dimension of the simulated fog was considered representative of natural fog because the effect of drop size is very small at these sizes, according to the model of Calder et al. (1996). Simulated fog has a uniform drop size and this is different to the drop size distribution of natural fog, but could be considered an homogeneous fog. If convection was 0.5 m s^{-1} and the mean concentration was 0.5 mg m^{-3} during three hours, then available water would be $0.54 \text{ mm (m}^{-3}\text{)}$ or $0.12 \text{ mm (m}^{-3}\text{)}$ in the case of radiative fog.

There are few reports regarding fog storage capacity by the vegetation (Jarvis, 2000), and the present work is the first to determine the storage capacity for a bromeliad. The results showed that drainage under natural conditions must be very difficult because the measured storage capacity is too high in comparison to natural fog fluxes reported for the region (Martorell and Ezcurra, 2002). Using stable isotopes Ingram and Matthews (1988) found that fog drip may be an important source of infiltration and groundwater recharge in an arid climate.

Photosynthesis and transpiration of shrub species such as *P. laevigata* are important during the morning, but under drought and dark conditions stomata remain closed (Hultine et al., 2003). Although the leaf area of *P. laevigata* and others is greater than that of *T. recurvata*, their interception storage capacity for fog, per unit of leaf area, must be smaller because the leaves of *A. farnesiana* and *P. laevigata* are glabrous and have a water-repellent waxy coat. In these conditions the presence of *T. recurvata* and their fog interception capacity could increase the availability of water for evaporation and decrease the vapor deficit of their host plants for longer during the early day.

Tillandsia recurvata could reduce soil erosion at the start of the rainy season, when most of the host shrubs are leafless in the semiarid climates. On the other hand, there are some

reports of pine forest decay allegedly to *T. recurvata* infestation. For terrestrial species that depend upon fog interception a water stress situation could develop in the presence of *T. recurvata*. While the causes of disordered growth of *T. recurvata* are multiple, availability of resources, such as water, is paramount.

Although these views appear to be contradictory, it is likely that the habitat of *T. recurvata* is changing due to global warming. In a catchment near the study area Gómez-Díaz et al. (2007) predicted increases of 57 to 62% in the arid climate and a reduction of 23% in the temperate area. Increased temperatures would allow *T. recurvata* to expand from lowland semiarid environments to higher altitudes where temperate forests are dominant. In addition, higher nocturnal temperatures due to climate change (IPCC, 2002), would reduce the chance of advective fog formation and increase the pressure on the availability of water resources.

4 Conclusions

The fog and rain data obtained under simulation showed the potential impact of *T. recurvata* on water relations where occult precipitation occurs. The interception storage capacity for rain was 0.19 mm which translates to 35.8 mm of annual rainfall. On the other hand, the fog interception storage capacity of 0.56 mm was much higher. However, the fluxes of natural fog probably are not enough to fill this capacity. Water detention after 1 h of wetting by fog was higher in darkness and therefore, stomata play an important role in water uptake. *Tillandsia recurvata* depends on their hosts to intercept fog and thus conserving complete natural ecosystems is important for water resource management. The benefits of *T. recurvata* related to reduced water uptake by shrubs, grass and herbs and the impact on soil conservation and aquifer recharge still need to be investigated.

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