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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, interception results in less water reaching the ground. However, fog drip or occult precipitation can result in negative interception because small drops are deposited on all plant surfaces and subsequently fall to the ground once vegetation storage capacities are exceeded. Fog drip is normally disregarded, 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 through applying simulated rain or fog. The storage capacity was proportional to dry weight mass. 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 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. Interception storage capacity (C_{\min}) was 0.19 and 0.54 mm for rainfall and fog respectively. *T. recurvata* contributed 20% to the rain interception of their shrub hosts: *Acacia farnesiana* and *Prosopis laevigata*. Meteorological data registered during one year at Cadereyta, México showed that radiative fog formation was possible during the dry season. The results showed the potential role of *T. recurvata* in capturing fog, which probably is a main source of water during the dry season that supports their reproductive and physiological activity at that time. 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 in the laboratory experiments it took up to 12 h to reach saturation conditions when fog was applied.

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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 content to humidity in the plant is low, the trichome wings are elevated and when moist, they are folded and stick to the leaf surface (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.

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

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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, Nívar and Bryan (1990, 1994) and Nívar 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 (Méndez et al., 2008). In addition to rainfall; atmospheric water, fog or dew are paramount for the biotic diversity in dry climates (Brown et al., 2008). The availability of water in these conditions is not abundant, but probably is sufficient to establish an independence from the soils' water relations; as in the case of epiphytic bromeliads (Reyes-García et al., 2008b).

Bromeliad species such as *Tillandsia recurvata* not only compete for space and light, but intercepted precipitation could have an influence on the amount of available water for: soil infiltration, surface runoff, or that for shrub and forest vegetations. The water detained and temporarily stored on the leaf is the fundamental process that controls the interactions between incident precipitation and vegetation. However, information is limited about the epiphyte interception storage parameters, which are needed in models that quantify the availability and distribution of water in ecosystems (Pypker et al., 2006). Furthermore, information on fog interception is scarce, especially for semiarid regions. With these antecedents, the objective of the present study was to determine the interception storage capacity of *T. recurvata* under simulated fog and rain. Laboratory experiments were used as an alternative to indirect field measurements where variable environmental conditions can introduce errors.

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2 Material and methods

2.1 Sites and laboratory setup

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 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, relative humidity, wind speed and air pressure 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. 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 during the dry season, at morning hours, from a site close to the laboratory facilities (20°43' N, 100°24' W).

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. The fresh mass of 30 plants was measured and a 99% confidence interval was constructed. The plants used in the experiments were collected from the field at random but considering that the fresh mass was within the established confidence interval.

The storage capacity of *T. recurvata* was directly determined in a laboratory with stable air temperature and relative humidity. 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

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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. 1). 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 0.26 L h^{-1} and 0.0004 mm mean drop size (Elehum 002, Sunshine Inc.). A timer switched on and off the humidifier as required. Inside the chamber a Hobo Pro sensor (Onset Corp.) recorded temperature and relative humidity (HR) every 5 min. A petri dish with water was placed inside the chamber to satisfy evaporative demand during the draining phase of the experiment.

2.2 Interception storage capacity

Intercepted rainfall is the amount of water returned directly to the atmosphere and not available for soil infiltration or runoff (Crockford and Richardson, 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; Putuhena 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).

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 lapsed for the draining phase. Maximum storage capacity was calculated as:

$$C_{\text{max}} = Wf_{\text{max}} - Wf_0 \tag{1}$$

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. The water available for draining was calculated as $C_{\max} - C_{\min}$. 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:

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

Thirty specimens were used to estimate the mean minimum interception storage capacity by rain. Spray was applied manually until the weight of the wetted specimen was constant. The drying phase was 12 h or until drainage finished.

2.3 Maximum water holding capacity

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 and D were determined as:

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

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2.4 Additional tests

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).

5 Therefore, the evolution of C was followed during 1 h of wetting with simulated fog and 12 h drying phase. Twelve plants were used, but only six plants were wetted. Afterwards, the daily change in fresh mass (ΔWf) was recorded for seven days for all plants. Plants were placed in the laboratory where the mean daily temperature was 22°C and HR was 30%.

10 All the tests described were performed regardless of time of day. 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. 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
15 daylight. During the day, stomata would be closed and therefore, plant mass should be lower than that of plants wetted at dark. ΔWf was recorded during the following seven days.

2.5 Interception scaling up

Potential storage capacities of *T. recurvata* in the vegetation were calculated as a function of Wf_0 (Pitman, 1989):
20

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

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

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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].

2.6 Dew point temperature

5 The data recorded during 2006 was used to explore the possibility of fog formation at the study sites. Although HR remains constant with altitude, the vapor pressure (e) and the saturation vapor pressure (e_s) does not. According to Monteith and Unsworth (1990) a factor of 4.81 was used instead of 6.11 to calculate dew point temperature (T_r):

$$10 \quad T_r = \frac{(-430.22 + 237.7 \times \ln(e))}{-\ln(e) + 19.08} \quad (7)$$

$$e = \frac{(\text{HR} \times e_s)}{100} \quad (8)$$

$$e_s = 4.81 \times 10.0^{\left(\frac{7.5 \times T}{237.7 + T}\right)} \quad (9)$$

where T is air temperature.

2.7 Statistical analysis

15 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 ΔW_f 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).

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3 Results and discussion

3.1 Laboratory experiments

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 $C_{\min} = 129.34 + 0.38 Wf_0$, $r^2 = 0.79$, $p \leq 0.0001$. However, the explained variance by Wf_0 was low probably because other variables were implied 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 and phenological conditions.

Table 1 presents storage coefficients obtained in the laboratory. The storage capacity was different between S' and C'_{\min} ($p = 0.03$). The values of C'_{\min} in relation to S' also suggested that drop size and aggregation are important for storage capacity and drainage (Sato et al., 2004). These authors reported similar S for leaf litter of species with trichomes or glabrous, but C_{\min} values were higher for the species with trichomes. In the present work, it was possible that coalescence increased drainage in the immersion tests for S' and therefore, C'_{\min} was higher for fog compared to rain ($p \leq 0.0001$). According to these results, water was better captured by *T. recurvata* when fog forms. However, natural fog in the study site probably was much smaller than the flows generated during the experiments. For example, stored fog during the first hour of simulation was 50% of Wf_0 and by the third hour it was 120% (Fig. 2). Jarvis (2000) reported the storage capacity of epiphytics after 30 h of fog simulation at 6.4 L h^{-1} as 5.94 times their dry weight whereas in the present work was 4.53 times after 12 h at 0.26 L h^{-1} .

There was no statistical difference in the daily weight change 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 ($-15.5 \pm 6.0 \text{ mg d}^{-1}$). Because the wetting occurred during daylight there was little opportunity for water to be absorbed. Probably, the stored water inside the plant before

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the test is the origin of this change in weight. However, specimens wetted for 1 h at dark gained more weight in comparison to wetting during daylight (543 ± 77 vs. 325 ± 56 mg, $p=0.048$). This result was interpreted as higher water detention inside the plant as a consequence of nocturnal stomatic opening during CO_2 assimilation since *T. recurvata* is a CAM species. Specimens wetted at dark lost less weight after the fog simulation and a 7 day drying period (-28 ± 63 vs. -244 ± 78 mg, $p=0.028$). Proportional to the initial fresh weight, the weight loss represented -1% and -15% , for dark and light conditions respectively. In these tests ambient HR was low and temperature constant; therefore, the plants could not gain weight during the drying phase. These results showed *T. recurvata* water relations depended upon recurrent conditions favorable for fog formation or condensation. 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.

3.2 Field study

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 ± 480 kg ha⁻¹ (Olalde and Aguilera, 1998). Scaled up C_{min} for rainfall was 0.19 mm for *T. recurvata* and 0.93 mm for the host shrubs *A. farnesiana* and *P. laevigata* (Mastachi, 2007). The contribution of *T. recurvata* to rainfall interception was calculated as 5% (35.8 mm) of the annual rainfall. In terms of fog, 57 min were needed to intercept 0.19 mm, this value was obtained using the relationship $C = -0.83 + 0.25 \ln(t)$, $r^2 = 0.98$, $p \leq 0.0001$; where t is time and C is the stored water in an area basis. However, 50% of the intercepted water, during one hour of fog wetting at daylight, was lost after 12 h of drying at low HR (Fig. 3).

Interpretation of such data depends on the real fog amount and adequate conditions for vapor condensation in the air surrounding the shrub vegetation. During 2006, these conditions existed during the dry season from November to April, when the lower T with

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respect to T_r (dew point temperature), indicated the possibility of condensation during early morning (Fig. 4). In June and July, T and T_r were similar, but fog could be formed if T_r is about 1 °C lower than T (Gultepe et al., 2007). In addition, 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. Fog and dew probably were not important during the rainy season because the difference between T and T_r was higher than 3.7 °C, although HR remained high. However, another factor important in fog formation is the evaporation from soil moisture and dew when the surfaces heat up (Gultepe et al., 2007). Nevertheless, 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.

3.3 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 ms⁻¹ and the mean concentration was 0.5 mg m⁻³ during three hours, then available water would be 0.54 mm (m⁻³) or 0.12 mm (m⁻³) 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. 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 probably is indirect.

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 or 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.

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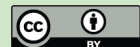
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4 Conclusions

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 (5%) of annual rainfall. On the other hand, the fog interception storage capacity of 0.54 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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Table 1. Interception storage capacity of *T. recurvata* in laboratory conditions.

	Immersion Mean	SE	Fog Mean	SE	Rain Mean	SE
(mg)						
Wf_0	1953	297	1453	116	2110	191
S	1783	353				
C_{\max}			2788	484		
C_{\min}			1610	329	942	444
(mg mg ⁻¹)						
S'	0.89	0.09				
C'_{\max}			2.04	0.26		
C'_{\min}			1.41	0.19	0.47	0.02
(mm)						
S	0.36					
C_{\max}			0.97			
C_{\min}			0.54		0.19	

Wf_0 : fresh biomass, S : maximum storage capacity, C_{\max} and C_{\min} : the maximum and minimum interception storage capacities, C'_{\max} , C'_{\min} and S' : the capacities per unit of fresh mass, SE: standard error of the mean.

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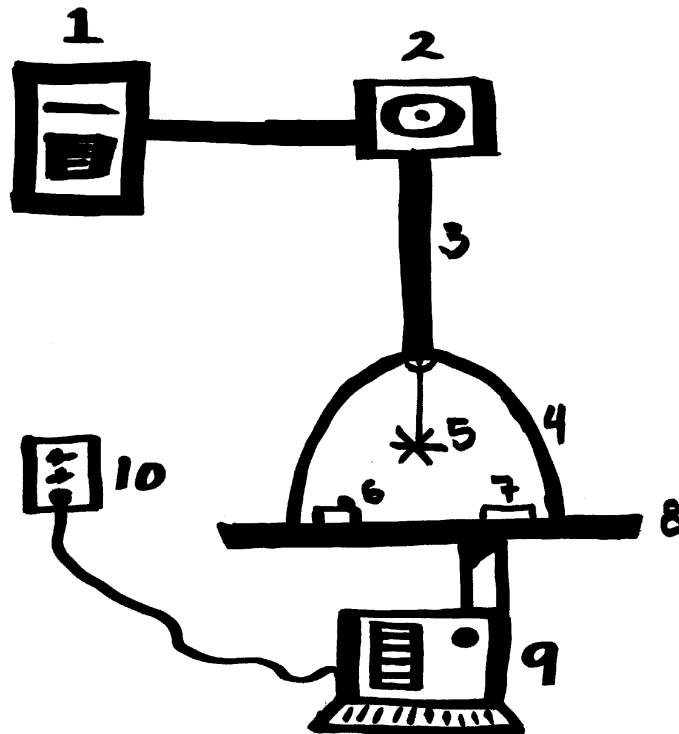


Fig. 1. Diagram of the fog simulation setup 1) computer, 2) electronic scale, 3) nylon line, 4) chamber, 5) *Tillandsia recurvata* sample, 6) humidity and temperature sensor, 7) petri dish, 8) metallic base, 9) humidifier, 10) timer.

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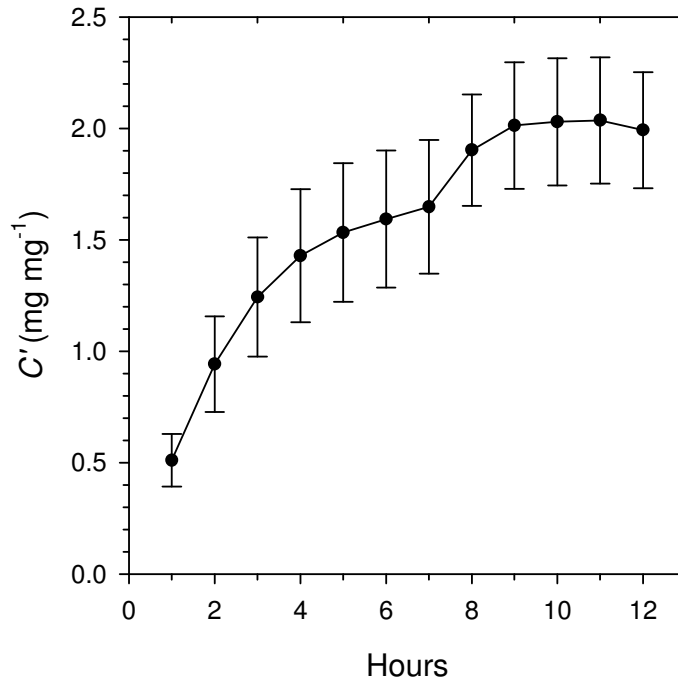


Fig. 2. Means and standard error of stored water in *T. recurvata* during 12 h wetting by simulated fog at $\geq 90\%$ HR and 22 °C.

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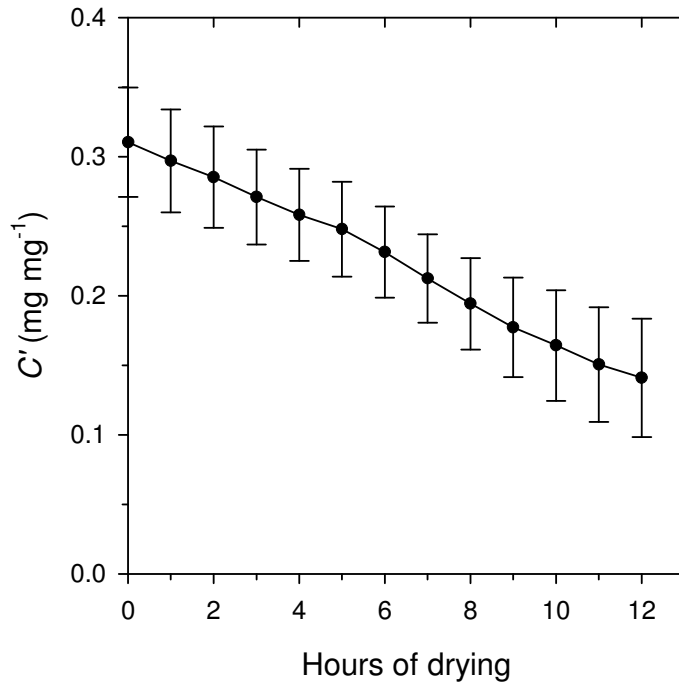


Fig. 3. Means and standard error of stored water in *T. recurvata* after 1 h wetting by simulated fog at $\leq 30\%$ HR and 22°C .

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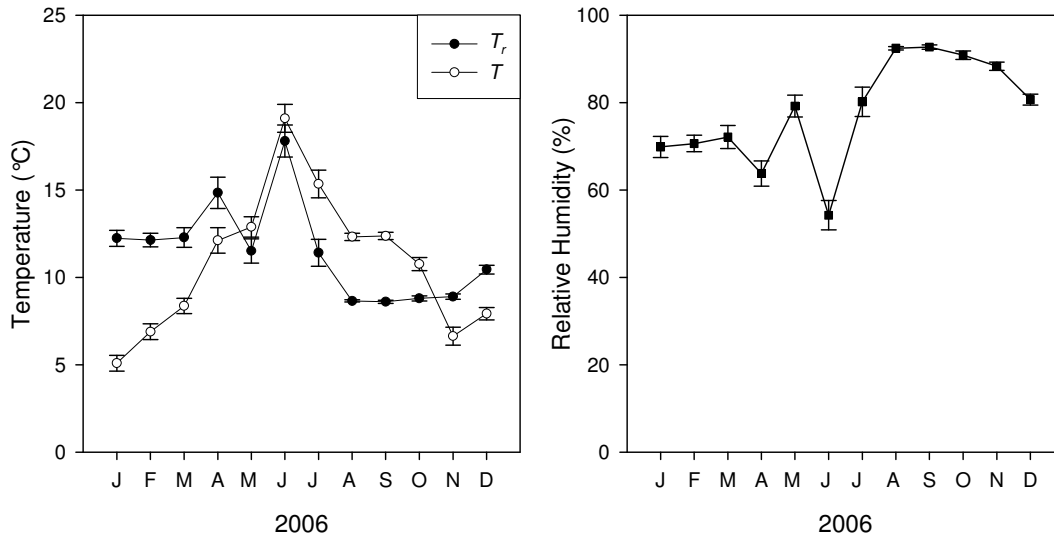


Fig. 4. Mean and 99% confidence interval for air temperature (T), dew point temperature (T_r) and relative humidity (HR) for morning hours 04:00 to 08:00 a.m. at the study sites.

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