

## Dew deposition on epiphytic bromeliad leaves: an important event in a Mexican tropical dry deciduous forest

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**Abstract:** Dew deposition was calculated for leaves of the epiphytic bromeliads *Tillandsia brachycaulos* and *T. elongata* in a tropical dry deciduous forest in Yucatán, Mexico, over one year. Plant characteristics and water relations were also measured. Estimations were made by using energy balance analysis and the Penman–Monteith equation. Dew accumulation was also quantified using a cloth-plate method and by change in mass of whole plants. Tissue water content and total leaf area were similar in the two species, but maximum tank water content was three-fold greater for *T. elongata* than for *T. brachycaulos*, which had a lower degree of tissue desiccation tolerance than *T. elongata*. Succulence for *T. brachycaulos* changed little during most of the year, decreasing significantly only during one month in the dry season. Leaf water potential and osmotic pressure did not change significantly after a dew-deposition event. Theoretical dew per night on leaves was greatest during the early dry season (about 0.72 mm) compared with 0.34 mm in the rainy season and 0.008 mm in the late dry season. Dew amounts alone are not adequate to support growth but may maintain a favourable water balance for epiphytic bromeliads during the driest months of the year.

**Key Words:** Bromeliaceae, crassulacean acid metabolism, energy balance, epiphytes, relative water content, succulence, *Tillandsia*, water relations, Yucatán

### INTRODUCTION

Epiphytic Bromeliaceae possess several adaptations to drought, specifically, succulence, water-impounding shoots (tanks), crassulacean acid metabolism (CAM), impermeable cuticles and foliar trichomes (Benzing 1990). For plants that grow in the canopy, with extreme moisture variations, stem succulence or water in the tank buffer such external changes and CAM allows for a high water-use efficiency. Trichomes, on the other hand, are an important vegetative feature of all Bromeliaceae and their ancestral function was perhaps water repellency (Pierce *et al.* 2001). In most epiphytic bromeliads, however, trichomes are specialized for water and nutrient absorption and can be very complex in structure. They consist of dead cells with outer cell walls rich in pectin, which capture moisture and conduct it rapidly into the mesophyll, allowing dry leaves of some atmospheric bromeliads to rehydrate within a few hours after wetting (Benzing 1990). However, water loss can also occur across the trichomes and the cuticle when stomata are closed. This can be substantial with up to 28% of the total water lost (Schmitt *et al.* 1989).

It seems that epiphytic bromeliads may also rely on alternative sources of water, such as fog or dew. For instance, in cloud forests, sites with higher fog intercep-

tion support more diverse and more abundant bromeliad populations (Cavelier & Goldstein 1989). Also, some species of *Tillandsia*, without functional roots, in Peruvian coastal deserts, grow predominantly with fog rather than rain as the moisture source (Benzing 1990).

A few laboratory or greenhouse studies of atmospheric bromeliads have determined that these plants are capable of obtaining water directly from the air whenever the relative humidity of the air is high (Martin 1994). In their natural environments, however, epiphytic bromeliads may often acquire water from the atmosphere in the form of dew, which could become an important water source, especially during the dry season (Smith *et al.* 1986). Humidity in the air may be high in tropical regions and because leaf temperatures can be lower than the air temperature at night, dew deposition on epiphytic bromeliad leaves could be a common event, even in dry deciduous forests. Additionally, CAM epiphytic bromeliads accumulate malic acid at night, increasing leaf tissue osmotic pressure and enhancing capacity for the absorption of dew (Griffiths 1988, Smith *et al.* 1986).

Although dew deposition on plant leaves has potential physiological consequences for some plants, it has received little attention. Dew has been shown to improve leaf water relations in pines and Mediterranean shrubs

(Boucher *et al.* 1995, Munné-Bosch *et al.* 1999), enhance survival of some species in tropical deciduous forest (Barradas & Glez-Medellín 1999) or even promote germination of some desert plants (Gutterman & Shem-Tov 1996). However, dew can also reduce nocturnal CO<sub>2</sub> uptake rates in some bromeliads (Benzing & Renfrow 1971, Martin 1994) and leaf wetting is positively correlated to fungal infection (Everts & Lacy 1990). Indeed, most research has been focused on the estimation and control of dew duration in crop fields to reduce rates of infection (Kimball *et al.* 1997, Luo & Goudriaan 2000, Wilson *et al.* 1999).

Dew deposition and duration on epiphytic bromeliad leaves was measured and estimated over 1 y in a tropical dry deciduous forest in the north of Yucatán, Mexico. Also, leaf water relations of the co-occurring *Tillandsia brachycaulos* and *T. elongata* were investigated during the same period. The results indicate that dew formation was quite frequent and could have an important role in the growth and survival of some epiphytic bromeliads.

## METHODS

### Study site and plant species

This study was conducted in the low tropical dry deciduous forest in the National Park of Dzibilchaltún (21° 05'N, 89° 35'W, 8 m altitude), Yucatán, Mexico. Mean annual rainfall and temperature are 700 mm and 25.8 °C, respectively (Thien *et al.* 1982). A marked dry season (March–May) is separated from the rainy season (June–October) by an early dry season, known locally as 'nortes' (November–February), characterized by up to 3-d events of strong winds (> 80 km h<sup>-1</sup>), little rainfall (20–60 mm) and low temperatures (< 20 °C; Herrera-Silveira 1995, Orellana 1999).

*Tillandsia brachycaulos* Schldl. occurs from southern Mexico to Venezuela (Smith & Downs 1977) and, at the study site, seedlings are abundant but most individuals (60%) persist by sympodial branching (Mondragón *et al.* 1999); *Tillandsia brachycaulos* also occurs in all other types of forest on the Yucatán Peninsula (Olmsted & Gómez-Juárez 1996). *Tillandsia elongata* Kunth var. *subimbricata* (Baker) L.B. Smith is restricted to the tropical deciduous forest of the northern part of the Yucatán Peninsula in Mexico (Olmsted & Gómez-Juárez 1996) and is common in similar forests in Trinidad, Cuba and Jamaica and in moist forests in Panama (Zotz & Ziegler 1997) and South America (Smith & Downs 1977). Both species exhibit CAM (Griffiths *et al.* 1986, Martin 1994); *Tillandsia brachycaulos* is an ecophysiological type V and considered an atmospheric, whereas *T. elongata* is type IV and shows a well-developed tank (Benzing 2000).

### Plant characteristics and water relations

All measurements were made on adult plants (8–10 cm height). Recently wind-displaced specimens were collected, brought to the Centro de Investigación Científica de Yucatán (CICY) Botanical Garden in April 2000, and placed on wooden sticks 2.5 m above the ground in a deciduous forest fragment. During the rainy season (June 2000), tissue water content and tank capacity were determined by weighing. Projected leaf area was measured from paper silhouettes and stable dry weight was determined after samples had been dehydrated at 65 °C (generally 24 h).

Relative water content (RWC) defined as (fresh weight – dry weight)/(turgid weight – dry weight), was determined for expanded leaves harvested from the middle rosette. Turgid weight was measured after hydrating the leaves for 24 h at 22 °C in plastic vials with distilled water and dry weight determined as above. The resaturation procedure of Oppenheimer & Catsky (1974) was used to evaluate the level of dehydration that tissues can tolerate. Leaf blades were harvested and left to desiccate at different times; initial RWC was then determined for samples from the dehydrated leaves, after which the samples were allowed to rehydrate for 24 h before final RWC was determined. Results are presented in a graph (final RWC vs. initial RWC) where the permanent turgor loss point is reached (Figure 1). Rehydrated leaf samples were tested for viability using neutral red on both tangential and transverse free-hand sections cut from the central portion of the leaves. Succulence, defined as water content per unit area, was measured monthly for *T. brachycaulos* and *T. elongata* from the same type of leaf (one leaf per plant, n ≥ 5 plants) in the field for a year; leaves were collected, their surface area determined, weighed and then dehydrated as described above. During the early dry and dry seasons of 2002, leaf water potential and osmotic pressure were measured before and after a dew deposition event occurred. Leaves were excised and cut in small pieces and the water potential was determined using a WP4 Dew-point PotentialMeter (Decagon Devices, Inc., Pullman, WA, USA). Leaf pieces were then crushed using a mortar, the tissue liquid was absorbed with filter-paper discs and its osmotic pressure determined using a Wescor C-52 sample chamber and an HR-33T microvoltmeter (Wescor, Logan, UT, USA). Monthly rainfall during the study period was obtained from a weather station at CICY (13.5 km south-west of Dzibilchaltún). During this study there were no fog events in the site.

### Dew-fall theory

Water vapour partial pressures ( $e$ ) at both air and leaf temperatures and water vapour pressure deficit ( $\delta e$ ) were obtained using equations from Jones (1992):

$$e = RH \times e_{s(T)} \tag{1}$$

where RH is the relative humidity and  $e_{s(T)}$  is the saturation partial pressure of water vapour at the temperature T in °C. The value of  $e_{s(T)}$  in kPa was approximated by the following empirical equation:

$$e_{s(T)} = a \exp [(bT)/(c + T)] \tag{2}$$

where T is in °C, and the coefficients a = 0.61121, b = 17.502 and c = 240.97. The vapour pressure deficit ( $\delta e$ ) was given by:

$$\delta e = e_{s(T)} - e \tag{3}$$

To obtain the rate of water deposition per unit area on a bromeliad leaf surface section, the Penman–Monteith equation was used (see Jones 1992):

$$J_{wv} = [s(\Phi_{ni} - C) + \rho_{as} C_p g_{HR} \delta e_1] / [\lambda(s + \gamma)] \tag{4}$$

where  $J_{wv}$  is the flux density of water vapour diffusing out of the leaf or, in this case, the water deposition rate (both phenomena are governed by the same physical principles), s is the slope of the curve relating saturation vapour pressure to temperature,  $\Phi_{ni}$  is the isothermal net radiation (equation 5), C is the leaf heat flux by conduction or convection (equation 6),  $\rho_{as}$  is the density of air saturated with water vapour,  $C_p$  is the specific heat capacity of air,  $g_{HR}$  is the total thermal conductance (equation 10),  $\delta e_1$  is the leaf-to-air vapour pressure difference,  $\lambda$  is the latent heat of vaporization and  $\gamma$  is the psychrometer constant ( $PC_p/0.622\lambda$ , where P is the atmospheric pressure). To obtain  $\Phi_{ni}$  the following equation was used (Jones 1992):

$$\Phi_{ni} = \Phi_n + g_R \rho C_p (T_{leaf} - T_{air}) \tag{5}$$

where  $\Phi_n$  is the net radiation (infrared irradiation absorbed – infrared radiation emitted),  $g_R$  is the radiation conductance (equation 10),  $T_{leaf}$  is the leaf surface temperature and  $T_{air}$  is the air temperature. The amount of heat across the leaf boundary layers and convected away was calculated as (Nobel 1991):

$$C = 2K^{air} (T_{leaf} - T_{air}) / \delta^{bl} \tag{6}$$

where  $K^{air}$  is thermal conductivity coefficient of air and  $\delta^{bl}$  is the average boundary layer thickness, which was calculated from the standard formula (Nobel 1991):

$$\delta^{bl}_{(mm)} = 4.0(l_{(m)} / v_{(m\ s^{-1})})^{1/2} \tag{7}$$

where  $\delta^{bl}$  is the average thickness of the boundary layer in mm,  $l_{(m)}$  is the average leaf dimension in the downwind direction in m (leaf width for both epiphytes), and  $v_{(m\ s^{-1})}$  is the ambient wind speed in  $m\ s^{-1}$ .

The net radiation at nighttime,  $\Phi_n$ , was obtained by subtracting (see Leuning 1989, Nobel 1991):

$$\text{absorbed infrared radiation} = a_{IR} \sigma [(T_{ground})^4 + (T_{sky})^4] \tag{8}$$

and

$$\text{emitted infrared radiation} = 2e_{IR} \sigma (T_{leaf})^4 \tag{9}$$

where  $a_{IR}$  and  $e_{IR}$  are the fraction of the infrared radiation absorbed and emitted by a leaf, respectively (considering the leaf as a black body,  $a_{IR} = e_{IR} = 1$ ),  $\sigma$  is the Stefan–Boltzmann constant,  $T_{ground}$  is the temperature of the ground and  $T_{sky}$  is the temperature of the sky. For equation 8, I considered the emitted infrared radiation from the ground for the lower leaf surface and the emitted infrared radiation from the sky for the upper leaf surface. To obtain  $g_{HR}$  the following equation was used (Jones 1992):

$$g_{HR} = g_H + g_R = D_H / \delta^{bl} + [4e_{IR} \sigma (T_{air})^3] / \rho C_p \tag{10}$$

where  $g_H$  is the heat conductance,  $D_H$  is the thermal diffusivity coefficient and  $\delta^{bl}$  is the average boundary layer thickness (Eqn 7).

The Penman–Monteith equation predicts that dew occurs when  $-s(\Phi_{ni} - C) > \rho_{as} C_p g_{HR} \delta e_1$  (Jones 1992). The rate of dew accumulation in  $m\ s^{-1}$  was calculated dividing  $J_{wv}$  by the water density at the air temperature. Dew deposition was calculated on an area basis of both leaf sides; trichomes are present on both sides of the leaves for these two epiphytic bromeliads and, for *T. elongata*, trichomes are very hydrophilic on both leaf surfaces (Pierce *et al.* 2001).

### Micrometeorological measurements

Microclimate and plant temperatures were monitored from May 2000 to February 2001 daily during at least 2 wk each month. Leaf temperatures were measured on one expanded leaf in the middle of the rosette from 5–10 plants of each species on exposed plants, which were on the southern part of the canopy, at 1.9–2.6 m from the ground level. A 0.08-mm-diameter copper-constantan thermocouple was attached with porous, adhesive tape to the abaxial surface of each leaf. Air temperature and humidity were measured with a Vaisala shielded probe (HMP35C-L, Campbell Scientific Inc., Logan, Utah, USA) and wind speed with a three-cup anemometer (Met One, Inc., Grants Pass, Oregon, USA). All data were sampled at 15-s intervals and average values were recorded every 10 min with a datalogger (CR21X, Campbell Scientific) equipped with a 16-channel multiplexer (AM416, Campbell Scientific). The radiative temperature of the sky (at each cardinal point at an angle of 45°) and surrounding vegetation temperature were measured with an infrared thermometer (Raynger, Raitek Co., Santa Cruz, CA, USA) every hour during the night and early morning for 5 d each season, but only before and after sunrise during the dry season.

### Quantification of dew deposition

During the early dry and dry seasons of 2002, dew was measured by a cloth-plate method suggested by Kidron (1998). Glass plates (10 × 10 × 0.2 cm) attached to plywood plates (10 × 10 × 0.5 cm) were used. A synthetic velvet-like square cloth (6 × 6 cm) was attached to the centre of the glass plate and a highly absorbent cloth (0.15 cm thick; commercially used for cleaning purposes) was placed above it. At dusk, the plates with weighed cloths were placed on plastic stands in the forest at varying heights: 0.01, 0.80, 1.95 and 2.85 m above the ground (four plates at each height). At dawn, cloths were collected with forceps and placed in small plastic bags, immediately sealed and later weighed in the laboratory. Some plates were covered from the cooling sky to estimate the amount of water collected by adsorption only. The amount of moisture was expressed as millimetres of dew.

Additionally, six plants of each species were collected, placed on a wooden stand (at 1 m above the ground) during the day at a total irradiance of  $4.23 \pm 0.52 \text{ mol m}^{-2} \text{ d}^{-1}$ , and during the night in an open room with a roof at ambient temperature, to prevent dew formation on their leaves, and their nocturnal water loss determined by weight each morning for three continuous days. Plants were then weighed and placed on plastic stands at dusk, at 2.85 m above the ground; a plastic cover was placed 2.5 cm above three plants of each species to avoid dew deposition. The next morning, plants were placed in plastic bags, sealed and weighed. Average water gain by dew was calculated as average dew deposited on the leaves minus average nocturnal water loss.

## RESULTS

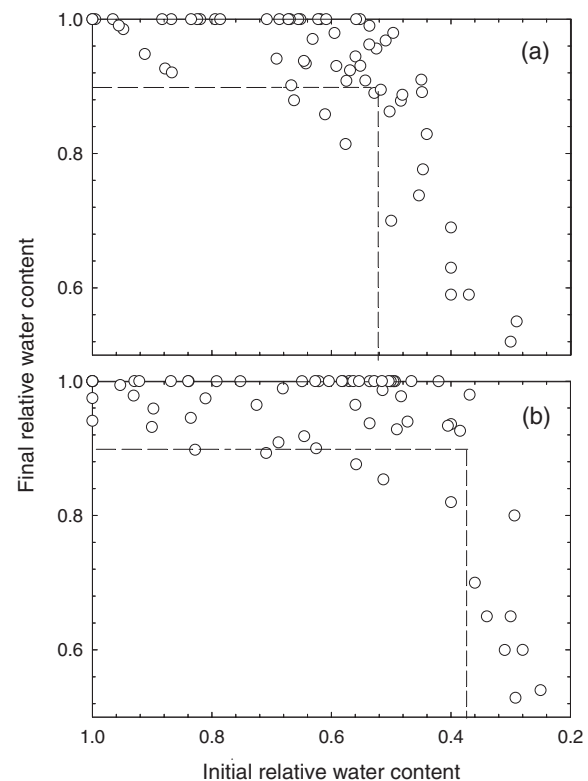
### Plant characteristics and tissue water relations

**Leaf and plant characteristics.** Plant water content and total leaf area for adult plants were similar for both *Tillandsia brachycaulos* and *T. elongata* (Table 1). Nevertheless, the maximum amount of water in all leaf bases of a plant (tank water content) for *T. brachycaulos* was about one third of that for *T. elongata* ( $P < 0.05$ ). Also, *T. brachycaulos* had about 20% greater specific leaf area than *T. elongata* ( $P < 0.05$ ; Table 1).

**Relative water content (RWC).** The relationship between the initial RWC and the final RWC after rehydration of the leaf tissues was described by a curve with an inflection

point where the tissues at low RWCs failed to recover (Figure 1); a 10% limit (dashed line in Figure 1) was used to determine this threshold (Oppenheimer & Catsky 1974). Leaf tissues of *T. brachycaulos* could recover after losing about 48% of their water content present at full turgor (Figure 1a), whereas the leaf tissues of *T. elongata* could lose over 62% (Figure 1b). About half of the cells in the leaves that were dried to below 40% of the water content at full turgor for both epiphytic species failed to accumulate neutral red stain.

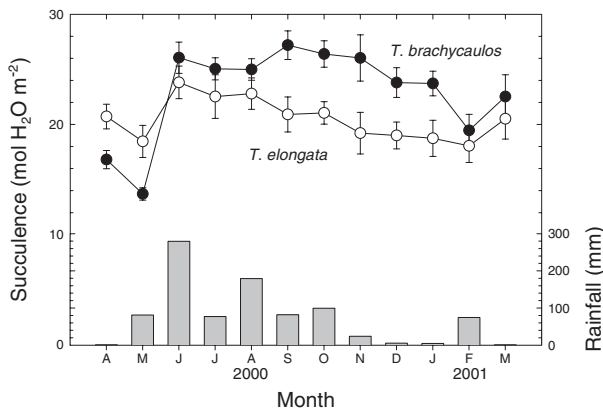
**Seasonal changes in succulence.** Succulence decreased during the dry season to about  $14 \text{ mol H}_2\text{O m}^{-2}$  for *T. brachycaulos* and  $18.5 \text{ mol H}_2\text{O m}^{-2}$  for *T. elongata* (Figure 2); however, it increased substantially at the start of the rainy season ( $26 \text{ mol H}_2\text{O m}^{-2}$  for *T. brachycaulos* and  $23.8 \text{ mol H}_2\text{O m}^{-2}$  for *T. elongata*) and remained high



**Figure 1.** Relationship between relative water content (RWC) before and after rehydration of the leaf tissues for (a) *Tillandsia brachycaulos* and (b) *T. elongata*. Dashed line indicates initial RWC after which most leaf tissues could not recover to 90% of their saturation RWC. Data are from 30 leaves of 10–15 plants.

**Table 1.** Morphological parameters for the epiphytic bromeliads *Tillandsia brachycaulos* and *T. elongata*. Values are means  $\pm$  SE ( $n \geq 5$  plants). Values within a column with a different superscript letter are significantly different (t-test,  $P < 0.05$ ).

Species	Plant water content (g)	Tank water content (g)	Total leaf area (cm <sup>2</sup> )	Specific leaf area (cm <sup>2</sup> g <sup>-1</sup> )
<i>T. brachycaulos</i>	8.70 $\pm$ 1.10	3.92 <sup>a</sup> $\pm$ 0.32	145.9 $\pm$ 11.6	87.20 <sup>a</sup> $\pm$ 3.16
<i>T. elongata</i>	8.08 $\pm$ 2.28	12.42 <sup>b</sup> $\pm$ 3.51	138.5 $\pm$ 31.5	68.14 <sup>b</sup> $\pm$ 7.28

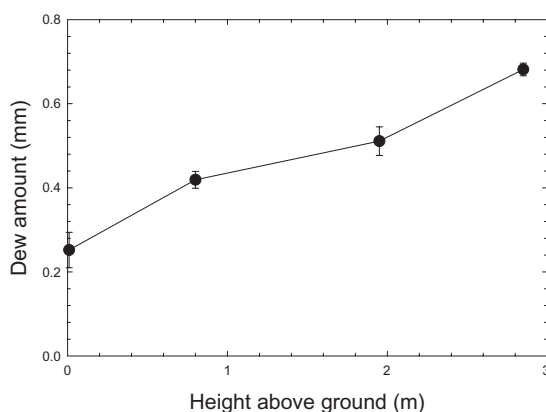


**Figure 2.** Succulence of *Tillandsia brachycaulos* (closed symbols) and *T. elongata* (open symbols) and total monthly rainfall (bars) during April 2000–March 2001. Data are means  $\pm$  SE ( $n \geq 5$  plants for *T. brachycaulos* and  $n = 3$  plants for *T. elongata*).

during most of the year. Succulence decreased slightly for both species (from 10 to 30%) during the early dry season (November–February), but it recovered when there was enough rain such as that occurred on 18 February 2001 (65 mm; Figure 2).

### Dew deposition and water potentials

Height above ground had an effect upon dew condensation using the cloth-plate method (Figure 3). During the early dry season, dew increased with height and maximal dew amounts occurred at 2.85 m above ground. However, dew collected on leaves for both species at the same height was about 98% less than the amount collected with the cloth-plate method (Table 2). The average nocturnal plant water loss for both species was about the same amount of dew deposited on their leaves; however, *Tillandsia elongata* showed almost twice the amount of water lost and dew deposited as *T. brachycaulos* (Table 2).



**Figure 3.** Dew amounts at four different heights during the early dry season 2002. Data are means  $\pm$  SE ( $n = 4$  dew collectors).

During the early dry season, osmotic pressures and water potentials of leaf tissues for both species did not show significant differences before and after dew deposition (Figure 4, upper panels). However, during the dry season, leaf osmotic pressure before and after dew deposition was significantly different for both species ( $P < 0.05$ , Figure 4, lower panels).

### Micrometeorological studies

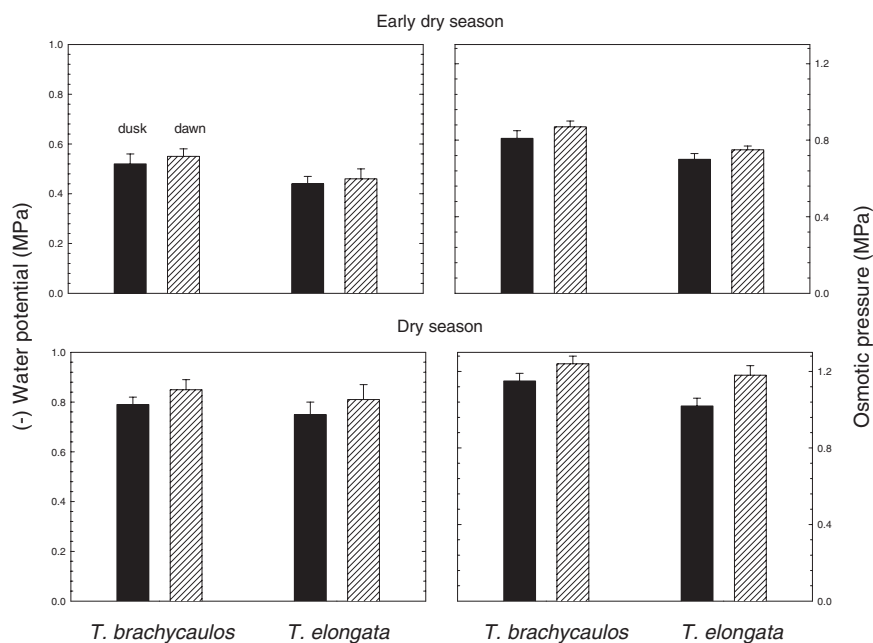
The temperature of fully expanded leaves of both *T. brachycaulos* and *T. elongata* was strongly coupled to variations in air temperature during the dry season (Figure 5a). During the daytime, leaf temperatures were higher than the air temperature but in the early afternoon, leaf temperatures fell below air temperature; wind speed increased two-fold after 14h00 LST. Leaf temperatures remained below air temperature during the night, and in the early morning, leaf temperatures of *T. elongata* were significantly lower than those of *T. brachycaulos* (inset, Figure 5a). Air vapour pressure ( $e$ ) was low during the daytime (down to about 2 kPa), and higher during the night (up to about 3 kPa after sunrise; Figure 5b). Also,  $e$  of the turbulent air ( $e$  at air temperature) did not change much during the morning and, for about an hour, was higher than the partial pressure in the leaf boundary layers (inset, Figure 5b); the difference between  $e$  at air temperature (in the turbulent air) and  $e$  at the leaf temperature (in the boundary layer and also the saturation partial pressure at that temperature) was higher for *T. elongata* than for *T. brachycaulos*.

During the rainy season, leaf temperatures were higher than air temperatures only briefly during the morning (from 06h00 to 09h30, Figure 6a) but they were much lower for the rest of the day and during the night. Almost every day, wind speed increased two-fold from 09h00 to 14h20 and three-fold from 14h30 to 15h40. During the early morning, leaf temperatures for *T. brachycaulos* and *T. elongata* were similar and about 1 °C lower than air temperature (inset, Figure 6a). Water vapour pressure was higher than  $e$  at the leaf temperatures during most of the night (Figure 6b) and the difference between  $e$  at air temperature and  $e$  at the leaf temperature was about 0.2 kPa and remained constant during the early morning (inset, Figure 6b).

During the early dry season, leaf temperatures were again higher than air temperature during most of the day and cooler during the late afternoon and night (Figure 7a). However, leaf temperatures were about 3–4 °C above air temperature during the hottest part of the day (from 11h00 to 15h00), despite wind speeds that were two–three-fold higher than during the night. During the early morning, leaf temperatures were about 1 °C below air temperature, and remained so for about 1 h after sunrise (inset, Figure 7a). Water vapour pressure was higher than  $e$  at air

**Table 2.** Theoretical dew deposition duration, average dew deposition per unit area ( $J_{wv}$ ) and water quantities deposited on leaves of *Tillandsia brachycaulos* and *T. elongata* during clear nights for the three contrasting seasons in the deciduous forest of Dzibilchaltún, Yucatán. Values of dew deposition on leaves are the dew amount collected minus the nocturnal plant water loss. Data are means  $\pm$  SE (n = 5 d).

Species	Season	Range of dew duration (h)	Average $J_{wv}$ (g H <sub>2</sub> O m <sup>-2</sup> s <sup>-1</sup> )	Theoretical dew deposition (mm)	Dew deposition on leaves (mm)
<i>T. brachycaulos</i>	Dry	0.8–1.0	0.002 $\pm$ 0.001	0.004 $\pm$ 0.001	–
	Rainy	10.0–11.5	0.008 $\pm$ 0.005	0.224 $\pm$ 0.007	0.084 $\pm$ 0.018
	Early dry	6.7–11.8	0.015 $\pm$ 0.003	0.754 $\pm$ 0.102	0.011 $\pm$ 0.001
<i>T. elongata</i>	Dry	1.5–2.3	0.003 $\pm$ 0.001	0.011 $\pm$ 0.007	–
	Rainy	10.0–11.0	0.014 $\pm$ 0.003	0.448 $\pm$ 0.024	0.092 $\pm$ 0.025
	Early dry	8.2–12.2	0.013 $\pm$ 0.002	0.680 $\pm$ 0.118	0.019 $\pm$ 0.007



**Figure 4.** Water potential (left panels) and osmotic pressure (right panels) of leaf tissues before (filled bars) and after (hatched bars) dew deposition, during the early dry (upper panels) and dry (lower panels) seasons of 2002. Data are means  $\pm$  SE (n = 5 plants).

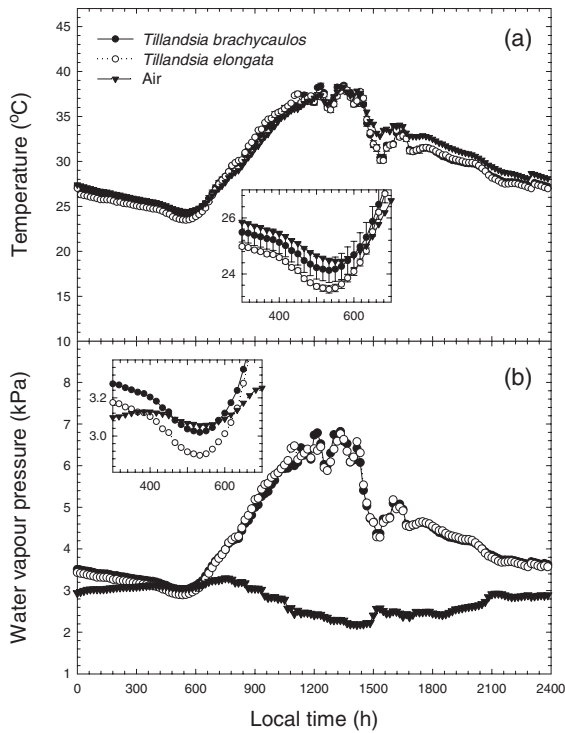
temperatures during most of the night until about 09h00 (Figure 7b). The difference between  $e$  at air temperature and  $e$  at leaf temperature was lower than that for the rainy season (about 0.18 kPa) but was approximately constant during most of the night (inset, Figure 7b).

### Dew duration and quantification

Dew deposition theoretically occurred for 0.8 to 11.8 h on the leaves of *T. brachycaulos* and for 1.5 to 12.2 h on leaves of *T. elongata* and varied with the season (Table 2). For instance, more hours of dew condensation occurred during the rainy and early dry seasons than during the dry season, when dew formed at most for 2 h during the night. Dew formed on about 50% of the sampled days during the dry season. In contrast, dew deposition could be observed every day during the rainy

season and during about 80% of the sampled days during the early dry season.

The average rate of dew deposition ( $J_{wv}$ ) during all seasons was similar for both *T. brachycaulos* and *T. elongata*, but was higher during the rainy and the early dry seasons than during the dry season (Table 2 and Figure 8). Although the periods of dew deposition during the rainy and early dry seasons were similar,  $J_{wv}$  was higher at night (before 24h00) and in the morning during the early dry season than during the rainy season. Also, during the early dry season,  $J_{wv}$  was high during the night, decreasing steadily until about an hour before sunrise and then increasing rapidly during sunrise; values above 0.001 g m<sup>-2</sup> s<sup>-1</sup> persisted for about 2 h after sunrise. For the rainy season,  $J_{wv}$  varied during the night but always reached the highest values before sunrise (Figure 8). The total amount of dew was twice as high for leaves of *T. elongata* than



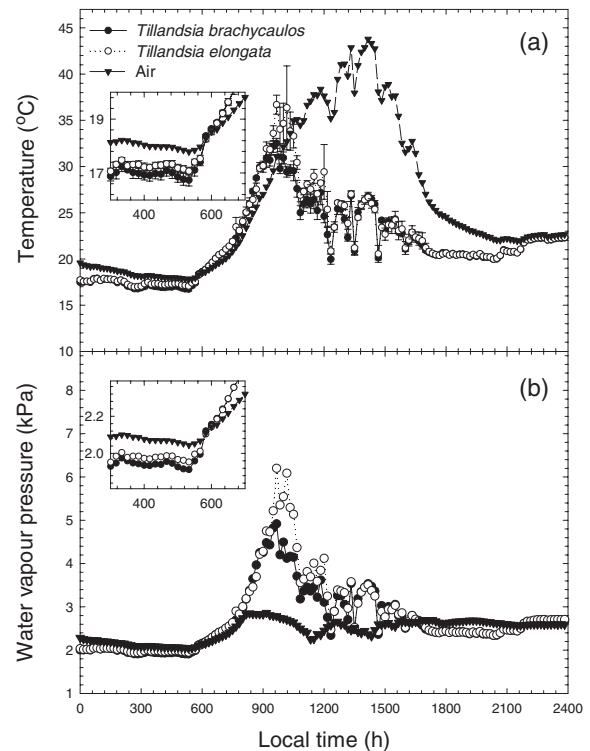
**Figure 5.** Daily courses of (a) air and leaf temperatures for *T. brachycaulos* and *T. elongata* and (b) water vapour pressure at air temperature and saturated vapour pressure at leaf temperatures during a clear day in the dry season (27 May 2000). The inset in (a) shows the air and leaf temperatures from 03h00 to 07h00 LST, and the inset in (b) shows the partial pressure of water vapour at air and leaf temperatures from 03h00 to 07h00 LST. Data for leaf temperatures are means  $\pm$  SE ( $n = 5$  plants).

for leaves of *T. brachycaulos* during the dry and rainy seasons (Table 2).

## DISCUSSION

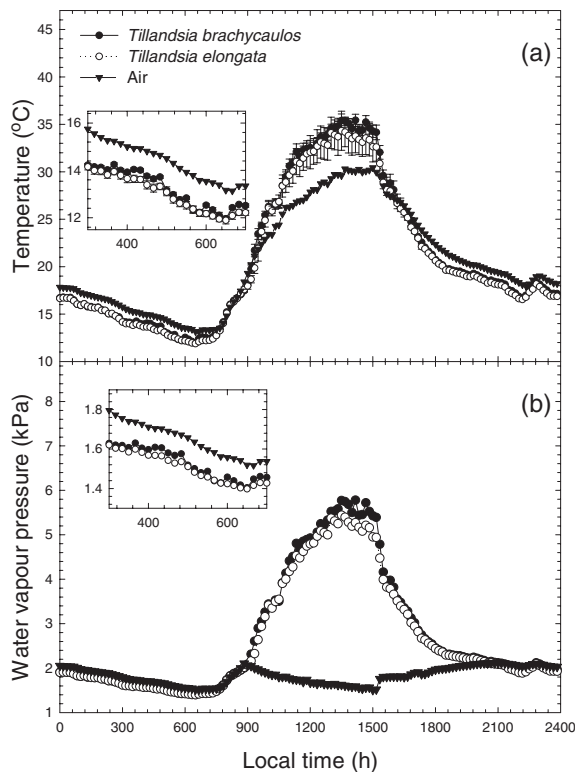
Maximum tank water content was significantly higher in *T. elongata* than in *T. brachycaulos* in agreement with a model developed to determine tank capacity for a suite of epiphytic bromeliads native to a Panamanian seasonal forest (Zotz & Thomas 1999). According to this model, adult plants of *T. brachycaulos* would need about 1.2 mm precipitation to fill their tanks and those of *T. elongata* about 1.8 mm. Surprisingly, the tolerance to tissue desiccation is lower for these two tillandsias compared with *T. fasciculata* and *Guzmania monostachya* in Panama (Zotz & Andrade 1998). However, *T. elongata* could dehydrate about 62% and still recover to a RWC of about 0.90, which about equals the performance of *T. fasciculata* in Panama (Zotz & Andrade 1998).

Succulence values for well-watered plants of *T. brachycaulos* and *T. elongata* were comparable to those for the epiphytic fern *Polypodium crassifolium* but were about a half of those for the epiphytic cactus *Epiphyllum phyllanthus* (Andrade & Nobel 1996, 1997). Succulence of *T.*



**Figure 6.** Daily courses of (a) air and leaf temperature for *T. brachycaulos* and *T. elongata* and (b) water vapour pressure at air temperature and saturated vapour pressure at leaf temperatures during a clear day in the rainy season (25 October 2000). The inset in (a) shows the air and leaf temperatures from 03h00 to 07h00 LST, and the inset in (b) shows the partial pressure of water vapour at air and leaf temperatures from 03h00 to 07h00 LST. Data for leaf temperatures are means  $\pm$  SE ( $n = 5$  plants).

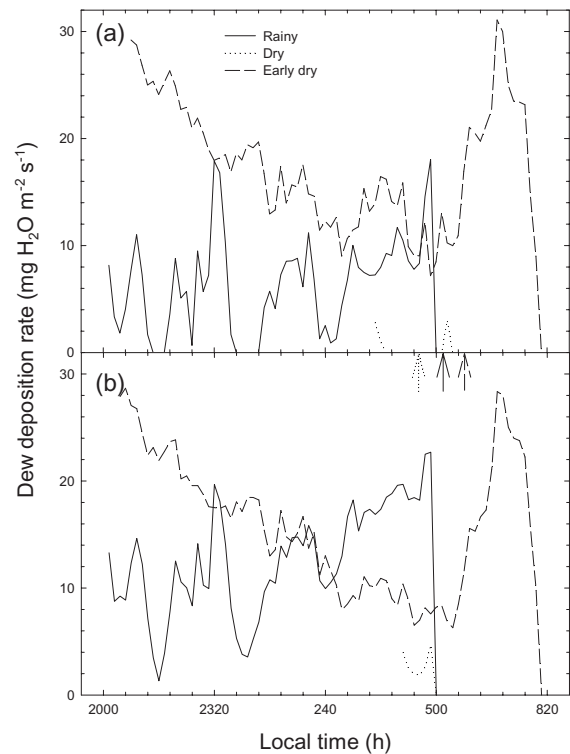
*brachycaulos* did not change during the rainy season and varied only slightly during the early dry season, decreasing from 24 to 19 mol m<sup>-2</sup> and recovering again to 22 mol m<sup>-2</sup> after a 64-mm rainfall event in February. Succulence of *T. elongata* decreased steadily during the early dry season from 21 to 18 mol m<sup>-2</sup> and also recovered rapidly to about 20 mol m<sup>-2</sup> after rain. Rapid rehydration recovery of succulence is common in epiphytes and occurs within a few hours to a few days after rewetting (Andrade & Nobel 1997, Sinclair 1983), and CAM epiphytes can also resume full acid rhythms within 3 d after rewetting (Andrade & Nobel 1996). Scarce rainfall together with the dew accumulated during most of the nights of the early dry season could help maintain sufficient hydration to support photosynthesis and growth of *T. brachycaulos*. Leaf production during the early dry season, which is about half of that occurring during the rainy season (Mondragón 2001), supports this hypothesis. Moderate growth during the early dry season may also reflect the favourable effects on CAM of the relatively abundant radiation (host trees are leafless), and the long nights and low night temperatures that prevail during this period of the year (Griffiths 1988, Nobel 1988).



**Figure 7.** Daily courses of (a) air and leaf temperature for *T. brachycaulos* and *T. elongata* and (b) water vapour pressure at air temperature and saturated vapour pressure at leaf temperatures during a clear day in the early dry season (15 January 2000). The inset in (a) shows the air and leaf temperatures from 03h00 to 07h00 LST, and the inset in (b) shows the partial pressure of water vapour at air and leaf temperatures from 03h00 to 07h00 LST. Data for leaf temperatures are means  $\pm$  SE ( $n = 5$  plants).

Despite the differences in leaf morphology and succulence between these two species, the values of leaf water potential ( $\Psi$ ) and osmotic pressure ( $\pi$ ) were similar for both species and comparable to those found in other epiphytic bromeliads (Smith *et al.* 1985, Stiles & Martin 1996, Zotz & Andrade 1998). After a dew deposition event in the early dry season,  $\Psi$  and  $\pi$  values did not change compared with those at dusk, which suggests that dew improved the leaf water balance in these species; in CAM plants,  $\Psi$  is lower and  $\pi$  is much higher at dawn than at dusk because of nocturnal acid accumulation (Nobel 1988, Smith *et al.* 1985). Also, during the dry season,  $\Psi$  decreased little and  $\pi$  was significantly higher for both species, suggesting that the dew amount was not enough to maintain water status. Moreover, nocturnal plant water loss can also be substantial in epiphytic bromeliads (Schmitt *et al.* 1989) so a prolonged dry season, with fewer dew deposition events than the rest of the year, could affect individual survival, especially of the less desiccation-tolerant *T. brachycaulos*.

During the rainy season, leaf temperatures of both *T. brachycaulos* and *T. elongata* were significantly lower



**Figure 8.** Dew deposition rate for (a) *Tillandsia brachycaulos* and (b) *T. elongata* during representative days from the dry, rainy, and early dry seasons. Arrows show the time when sunrise occurred for each season. Data are for clear days and correspond to days from Figures 3, 4 and 5, respectively.

during clear days, indicating evaporative cooling. Few studies with CAM epiphytes report water loss during the daytime. For example, although the maximum transpiration rate ( $J_{wv}$ ) of well-watered plants of the epiphytic cacti *Epiphyllum phyllanthus* and *Rhipsalis baccifera* can also be high in the late afternoon and shifts to the night after 2 wk of drought (Andrade & Nobel 1997), the maximum  $J_{wv}$  in these epiphytic bromeliads occurred early in the morning. Martin & Schmitt (1989) and Schmitt *et al.* (1989) report high rates of water loss throughout the day in *T. usneoides* and *T. recurvata*, respectively, and suggest that this occurs from leakage through the trichomes. Most reported field  $CO_2$  measurements have been made on epiphytic bromeliads only during the dry season (Griffiths *et al.* 1986, Lüttge *et al.* 1986) and indeed, in one of these studies (Lüttge *et al.* 1986), the epiphytic bromeliad *Aechmea lingulata* showed a high  $J_{wv}$  in the afternoon, after a rainy day during the dry season in Trinidad. Even though CAM plants generally have maximal stomatal opening earlier in the night under well-watered conditions (Nobel 1988), there are a few reports on constitutive CAM plants converting to daytime  $CO_2$  uptake when well-watered (Hartsock & Nobel 1976).

Dew deposition has been measured or estimated in several ecosystems (Jacobs *et al.* 2000, Kimball *et al.* 1997,



Malek *et al.* 1999, Wilson *et al.* 1999) but rarely in the tropics (Barradas & Glez-Medellín 1999, Luo & Goudriaan 2000). Dew deposition in the desert ranges between 0.1–0.3 mm per night (Jacobs *et al.* 2000) and in a tropical dry deciduous forest in Western Mexico ranged from 0.04 to 0.36 mm per night at different levels within the forest, during the dry season (Barradas & Glez-Medellín 1999), which agreed well with the dew deposition measured and estimated in this study during the dry and rainy seasons. However, the relatively low values obtained when measuring dew on whole plants suggest either that maximal dew deposition values occurred in small leaf sections or that some dew can drain off the plant to the branches or the ground. The relatively high theoretical and measured values during the early dry season can be explained by the onshore movement of humid air from the north (Orellana 1999), longer nights, when dew deposition could occur for up to 12 h, and the lower leaf and air temperatures, which lead to higher relative humidities. Moreover, the two highest deposition rates occurred during the early night and before sunrise, which are the times when the relative humidity is highest because of afternoon rains and predawn low temperatures.

The amount of dew theoretically deposited on leaves of *T. elongata* was greater than that on leaves of *T. brachycaulos* during the dry and rainy seasons. The thinner leaves of *T. elongata* were, most of the time, cooler than the thicker and narrower leaves of *T. brachycaulos* and thus experienced greater differences in partial vapour pressure with the air. *Tillandsia elongata* was assigned by Pittendrigh (Griffiths & Maxwell 1999) to his 'sun' group of bromeliads, indicating that it grows near the top of the canopy. In fact, in Dzibilchaltun, *T. elongata* occurs more often at the top of the canopy (pers. obs.) whereas most individuals of *T. brachycaulos* grow deeper within the crown (Mondragón 2001). Moreover, the tissues of *T. elongata* can tolerate more desiccation than those of *T. brachycaulos*. Being at the top of the canopy allows *T. elongata* to receive more rainfall, light and dew than *T. brachycaulos*.

More studies need to be done with other epiphytic species to assess the significance of dew and other non-rainfall sources of water in their water balance. For example, mist and fog are the primary source of water during the epiphytic stage of the hemi-epiphyte *Didymopanax pittieri* in a cloud forest (Feild & Dawson 1998), where clouds and mist deliver up to 356 mm or about 8% of the annual total precipitation (Clark *et al.* 1998). Similarly, during this study, dew was estimated to represent about 10% of the annual total precipitation (including dew and rainfall), although evaporation in this dry deciduous forest is much higher than in cloud forests. In any case, dew may constitute a substantial source of water for *T. brachycaulos* and *T. elongata* through much of the year and could help these bromeliads tolerate water vapour

pressure deficits at our study site that can be as high as 7 kPa during the day. Certainly, the amount of dew deposited on bromeliad leaves is not enough to maintain growth and survival but the amount and duration of dew may aid growth and survival of epiphytic CAM bromeliads in tropical dry deciduous forests.

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