Dew Can Prolong Photosynthesis and Water Status During Drought in Some Epiphytic Bromeliads From a Seasonally Dry Tropical Forest

Authors: Chávez-Sahagún, Eduardo, Andrade, José Luis , Zotz, Gerhard, and Reyes-García, Casandra

Source: Tropical Conservation Science, 12(1)

Published By: SAGE Publishing

URL: https://doi.org/10.1177/1940082919870054

Research Article

Dew Can Prolong Photosynthesis and Water Status During Drought in Some Epiphytic Bromeliads From a Seasonally Dry Tropical Forest

Tropical Conservation Science
Volume 12: 1–11
© The Author(s) 2019
Article reuse guidelines:
sagepub.com/journals-permissions
DOI: 10.1177/1940082919870054
journals.sagepub.com/home/trc
SAGE

Eduardo Chávez-Sahagún[1], José Luis Andrade[1], Gerhard Zotz[2], and Casandra Reyes-García[1]

Abstract

Dew can represent an alternate water source in epiphytic bromeliads. However, the physiological relevance of dew to withstand the dry season, within seasonal forests, is not fully understood. To study the effect of dew deposition in the physiological response of four *Tillandsia* species with contrasting morphologies, we performed an experiment in the tropical dry deciduous forest of Dzibilchaltún, Mexico, during the transition from the wet to the dry season. Half of the individuals were covered every night with a plastic tarp to prevent dew deposition. Environmental variables were monitored, and physiological variables (relative water content, leaf succulence, nocturnal tissue acidification and electron transport rate) were measured at the beginning and end of the experiment. We found that throughout the drought, there was consistent nighttime dew formation for >4 h. Both the time the leaves spent at a temperature below dew point of the air and the effect on water and carbon metabolism was species -specific, as evidenced by the comparison among the exposed and covered (dew -deprived) plants. *Tillandsia elongata* and *Tillandsia brachycaulos* had longer times of dew formation and showed higher water content at the end of the experiment when exposed to dew, the latter species also had a significant effect of dew on nocturnal acidity. In contrast, neither *Tillandsia yucatana* nor *Tillandsia fasciculata* seemed to be using dew as a relevant source of water during the dry period. We discuss the species' morphoanatomical traits that may be related to the differences in dew formation and use.

Keywords

alternate sources of water, Bromeliaceae, dew, drought, crassulacean acid metabolism, Tillandsia, water budget

Introduction

Approximately half of the Bromeliaceae are epiphytes, making it the second most important angiosperm family in terms of the number of epiphytic species (Zotz, 2013). In the canopy habitat, epiphytic bromeliads endure periods of drought interspersed by pulses of moisture input (Andrade, 2003; Martin, 1994; Reyes-García, Mejia-Chang, & Griffiths, 2012; Zotz & Hietz, 2001). To cope with these conditions, these species display an array of morphological and physiological traits aimed at acquiring, storing, and conserving water. These include succulent leaves, water impounding "tanks," and crassulacean acid metabolism (Benzing, 2000; Crayn, Winter, & Smith, 2004; Dodd, Borland, Haslam, Griffiths, & Maxwell, 2002; Martin, 1994). In addition, another important feature is the presence of foliar trichomes, which are highly hygroscopic, scale-like, multicellular structures that absorb water

---

[1]Unidad de Recursos Naturales, Centro de Investigación Científica de Yucatán, Mérida, Yucatán, México
[2]Institute for Biology and Environmental Sciences, Functional Ecology, Carl von Ossietzky University Oldenburg, Germany

Received 7 June 2019; Revised 16 July 2019; Accepted 23 July 2019

Corresponding Author:
Casandra Reyes-García, Unidad de Recursos Naturales, Centro de Investigación Científica de Yucatán, A.C. Calle 43 No. 130. Col. Chuburná de Hidalgo, C.P. 97205 Mérida, Yucatán, México.
Email: creyes@cicy.mx

and nutrients (Benzing, 2000; Benzing, Henderson, Kessel, & Sulak, 1976; Givnish et al., 2014).

Epiphytic bromeliad species mainly conform to one of two functional groups: "tank" and "atmospheric" species (Benzing, 1990; Pittendrigh, 1948), which reflect two distinct ecological and physiological strategies. In tropical dry deciduous forests, tank species are rare because their tolerance to drought, once tank water is exhausted, is limited; so these plants show a more conservative use of water (Graham & Andrade, 2004; North, Lynch, Maharaj, Phillips, & Woodside, 2013; Pittendrigh, 1948; Reyes-García, Griffiths, Rincón, & Huante, 2008; Reyes-García et al., 2012; Wolf & Alejandro, 2003). Both tank and atmospheric epiphytic bromeliads from seasonal environments can display succulent leaves with a dense cover of well-developed trichomes (Benzing, 2000). Yet, atmospheric species, which are more common in these dry forests, usually show higher leaf succulence and are better adapted to use water from rain pulses. Also, atmospheric species are capable of maintaining photosynthetic activity under low leaf relative water content (RWC; Benzing, 2000; Cach-Pérez et al., 2013; Lüttge, 1989; Pierce, 2007; Reyes-García et al., 2012).

Apart from rain, epiphytes may rely on dew and fog as alternate sources of water, which influences their abundance, vertical and altitudinal distribution, and survival (Andrade, 2003; Cavelier & Goldstein, 1989; Guevara-Escobar et al., 2011; Rapp & Silman, 2014; Reyes-García et al., 2008). Dew deposition generally occurs during nighttime at high humidity and relatively low temperature. When the air adjacent to the leaves cools down to its dew point, and leaf surfaces get colder than that surrounding air, water will condense on those surfaces (Nobel, 2009).

Fog and dew can be the main source of water in bromeliads from arid environments (González et al., 2011; Pinto, Barría, & Marquet, 2006). However, the relative importance in the total budget of dry forests epiphytes seems to vary greatly between species, location, and season (Andrade, 2003; Graham & Andrade, 2004; Reyes-García et al., 2008, 2012; Wu et al., 2018). The few studies that have explored the importance of dew and fog have found that the ability to access, intercept, and use these water resources may depend on plant morphology and physiology (Graham & Andrade, 2004; Martorell & Ezcurra, 2007; Reyes-García et al., 2012). Yet, the magnitude of the effect of dew deposition on the physiology of epiphytic species *in situ* remains to be quantified, as the question to its actual relevance in plant survival remains unanswered.

This study evaluated the importance of dew deposition in the physiological response of four epiphytic *Tillandsia* species with contrasting life forms (from tank to atmospheric) in the tropical dry deciduous forest of Dzibilchaltún, Mexico. A field experiment was setup during the transition from the early dry season, locally known as "nortes" characterized by daily low temperatures, wind events, sparse rainfall, and dew deposition (Andrade, 2003; Orellana, 1999), to the dry season. To do so, we monitored the physiology of the species during this transition, either under natural conditions or under semicontrolled conditions where plants were covered with a plastic tarp during the night to prevent dew formation.

We expected that because of this seasonal transition, the tank species would show a more marked decrease in photosynthetic activity, with more pronounced changes in RWC and leaf succulence than atmospheric species. We also expected that dew-deprived plants would show significantly lower photosynthetic activity and water status values in comparison to the plants exposed to dew deposition.

Materials and Methods

Study Site and Plant Species

This study was conducted at the Dzibilchaltún National Park (21° 05′N, 89° 35′W, 8 m a.s.l.), Yucatan, Mexico, which is characterized as a tropical dry deciduous forest with a mean annual rainfall of 700 mm and mean temperature of 25.8°C (Thien, Bradburn, & Welden, 1982). A marked dry season (March–May) is separated from the wet season (June–October) by an early dry season known locally as "nortes" (November–February). The latter is characterized by scattered rainfall, low nocturnal temperatures (<20°C), and dew formation (Herrera-Silveira, 1995; Orellana, 1999).

Four epiphytic bromeliad species of the genus *Tillandsia* were selected: the shallow tank *Tillandsia elongata* Kunth; *Tillandsia fasciculata* Sw., which is variously described as an atmospheric, a tank or an intermediate species (Bader, Menke, & Zotz, 2009; Cach-Pérez, Andrade, Cetzal-Ix, & Reyes-García, 2016; Cach-Pérez, Andrade, & Reyes-García, 2018; Pittendrigh, 1948; Zotz & Thomas, 1999); *Tillandsia brachycaulos* Schltdl., an atmospheric generalist with a limited water impounding capacity; and *Tillandsia yucatana* Baker, an atmospheric with very succulent leaves and no water impoundment. All species are obligate epiphytes with crassulacean acid metabolism and are native to the study site (Cach-Pérez et al., 2013; Ramirez-Morillo, Carnevali, & Chi May, 2004). Species differ strongly in morphology, ecological type, and distribution range along the Yucatan Peninsula (Figure 1 and Table 1). Most of the species are rare at the study site (Cach-Pérez et al., 2013; Chilpa-Galván, Tamayo-Chim, Andrade, & Reyes-García, 2013), a protected area. Thus, apart from *T. brachycaulos*, which was collected at Dzibilchaltún, plants were

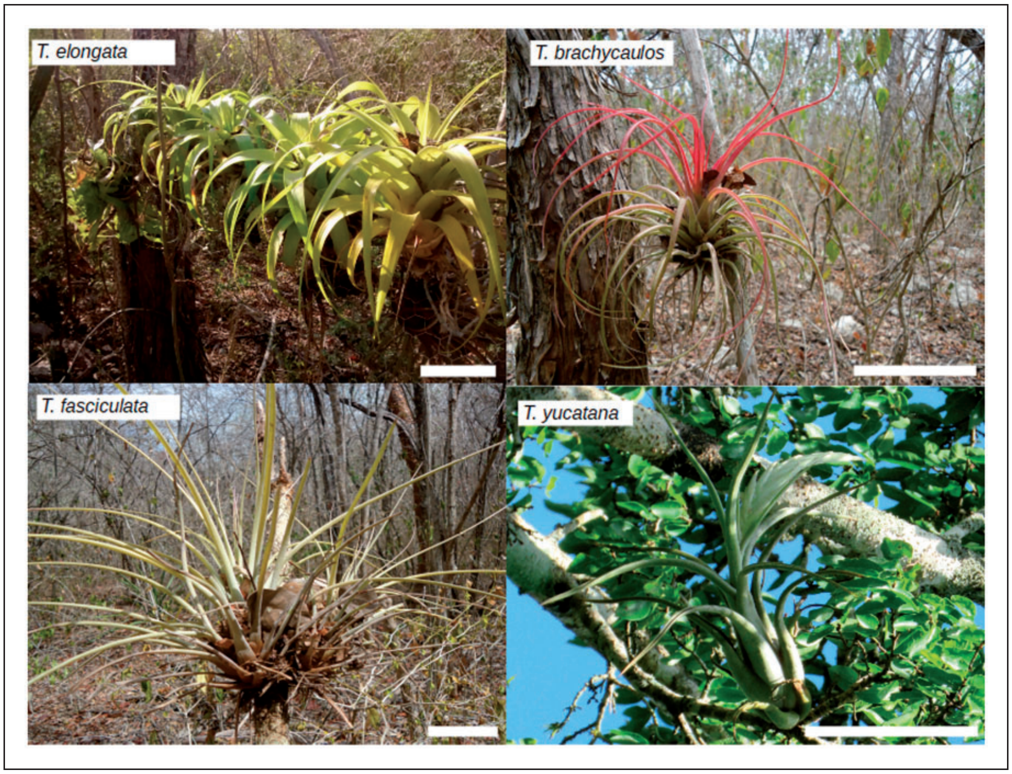

Figure 1. The epiphytic *Tillandsia* species with contrasting morphologies and life forms selected for this study. The white bars are 10 cm. Adapted from *Tillandsia yucatana* by C. Espadas-Manrique, others by E. Chávez-Sahagún.

Table 1. Life form, water impounding capacity, Leaf Size (Length × Width), Specific Leaf Area (SLA, $cm^2\ g^{-1}$) and Habitat on the Yucatán Peninsula for the Species Used in This Experiment.

Species	Life form	Water impounding capacity	Leaf size (cm × cm)	SLA ($cm^2\ g^{-1}$)	Habitat[2]
T. elongata	Tank	Yes	$31 - 39 \times 2.5 - 5$	99.5 ± 7^a	DF, SD
T. fasciculata	Atmospheric	Yes	$34 - 58 \times 2 - 3$	48.4 ± 1^b	DF, SD, SE
T. brachycaulos	Atmospheric	Reduced	$25 \times 0.5 - 1.9$	106.3 ± 7^b	DF, SD, SE
T. yucatana	Atmospheric	No	$5–15 \times 3 - 7$	36.2 ± 2^c	CD, SM, DF

Note. CD = coastal sand dune; DF = deciduous forest; SD = semideciduous forest; SE = semievergreen forest; SM = scrub mangrove. Different letters indicate significant differences in SLA, $p < .05$.

[1] Ramirez-Morillo et al. (2004).

[2] Cach-Pérez et al. (2013).

collected elsewhere: *T. elongata* was collected at Homún; *T. fasciculata* at Hopelchén; and *T. yucatana* at Komchén, all three sites within the Yucatan Peninsula. Plants, which were adult size, were kept in a shade house at the Centro de Investigación Científica de Yucatán (located <10 km from Dzibilchaltún) for a week before the experiment.

The experiment was established at a site with abundant epiphytes in December 2015. A group of 12 to 16 individuals per species were mounted on a wire mesh 1.2 m above the ground. The plants were placed evenly spaced in two rows, with the smaller atmospheric species above the larger tank species to prevent shading effects. The plants had been receiving natural rain at the site or nearby shade house and were watered to reduce stress from manipulation when mounted. After 36 days of acclimation (during which no rain was registered at the site), half the plants of each species were covered daily with a plastic tarp during nighttime (18:00 to 06:00 h) to prevent dew deposition on the leaves; the rest of the plants were left uncovered (Supplementary Material). The covered treatment isolated the air to prevent condensation, but encompassed all the plants in the treatment together, thus ensuring a large amount of air within the enclosure so that nighttime gas exchange was not impaired. The experimental treatment lasted 8 weeks from late January to mid-March 2016.

To isolate the effect of dew, leaf wetting from rainfall was minimized. During this period there was only one important rainfall event on March 13 (12.7 mm); to prevent plants from getting wet, all plants, irrespective of treatment, were covered with two plastic tarps before the event started. Minor rainfall events (1–3 mm), occurred during January (five events) and February (one event; data from a CONAGUA meteorological station); however, no measures were taken in such instances.

Microenvironment Measurements

Air temperature and relative humidity were recorded hourly using iButtons (Maxim iButton, Silicon Valley, USA), which were placed at the same height as each group of plants. Vapor pressure deficits were calculated after Jones (1992). Leaf temperature was measured with thermocouples attached to the underside of leaves with microporous tape; temperature was measured every minute and averages recorded every 10 min using a datalogger (CR21X, Campbell Scientific, North Logan, USA). To measure the duration of dew events, two leaf wetness sensors (Model 237 Leaf Wetness Sensor, Campbell Scientific, North Logan, USA) were affixed to the wire mesh along the plants in each treatment, averages recorded every 10 min with the same datalogger.

The dew point of the air (t_d) was calculated after Lawrence (2005):

$$t_d = \frac{B_1\left[ln\left(\frac{RH}{100}\right) + \frac{A_1 t}{B_1 + t}\right]}{A_1 - ln\left(\frac{RH}{100}\right) - \frac{A_1 t}{B_1 + t}}$$

where RH is the relative humidity, t is the air temperature, and $A_1 = 17.625$, and $B_1 = 243.04°\mathrm{C}$. The theoretical duration of dew deposition was calculated as the time when leaf temperature was $\leq$ air dew point.

Physiological Data

The effect of dew deposition on plant physiology was assessed by determining nocturnal acidification, RWC, leaf succulence, and electron transport rate (ETR) in late January just before beginning the nightly covered treatment (referred to as early dry season), and in mid-March after the plants had been under the treatment for 8 weeks (referred to as dry season). All physiological measurements were carried out on 5 to 8 young, but fully expanded healthy leaves per species per treatment. To characterize RWC, leaf samples were collected before dawn and placed in a sealed bag with moist tissue paper and transported in a cooler with ice to the laboratory to obtain fresh weight, and then placed in distilled water for 48 h to obtain saturated weight. Leaves were then scanned, and leaf area was estimated using ImageJ software. After drying at 65°C for 48 h, dry weight was determined. RWC was calculated as follows: (fresh weight – dry weight)/(saturated weight – dry weight) × 100; leaf succulence was calculated as ([fresh weight – dry weight] × 1,000)/leaf area. To further characterize relevant traits that may differentiate the species, we measured specific leaf area (SLA) as follows: (leaf area [cm^2])/(dry weight [g]), at the beginning of the experiment.

To estimate nocturnal acidification (ΔH^+), samples from every plant of each species were collected at sunset and before dawn the next day and frozen in liquid N_2 on site. In the laboratory, samples were first weighed and then macerated in a porcelain mortar and boiled in distilled water for 5 min. After cooling to room temperature, samples were titrated with sodium hydroxide (0.01 N NaOH) using an automatic titrator (702 SM Tritino, Metrohm, Switzerland). Acidity at dawn minus acidity at sunset is reported as ΔH^+ and expressed in mmol H^+ g^{-1} fresh weight.

Chlorophyll fluorescence was measured in the field with a pulse amplitude-modulated fluorometer (Mini-PAM, Walz Effeltrich, Germany). Light response curves were performed in dark-adapted leaves to assess maximum ETR ($\mathrm{ETR}_{\max}$) values. ETR was calculated after Maxwell & Johnson (2000):

$$\mathrm{ETR} = \Phi_{\mathrm{psII}} \times \mathrm{PFDa} \times (0.5)$$

where Φ_{psII} is the quantum yield of photosystem II, PFDa is absorbed photon flux density, and 0.5 accounts for the partitioning of energy between PSII and PSI. Values of leaf light absorption or absorptance were obtained from the mid-leaf section of recently excised leaves from plants used in this experiment ($n = 5$) using a ultraviolet/visible/near infrared Lambda 900 spectrometer coupled with a PELA9026 integrating sphere (Perkin-Elmer, MA, USA). Absorptance values (a) used were as follows: *T. elongata* = 0.72, *T. fasciculata* = 0.65, *T. brachycaulos* = 0.67, and *T. yucatana* = 0.78.

Statistical Analyses

Linear regressions were performed to assess the relationship between average nocturnal relative humidity, air temperature, or vapor pressure deficit, and the days passed from the beginning of the experiment. Repeated measures analyses of variance (ANOVAs) were used to analyze the effect of the season, species, and treatments on the duration of dew deposition, RWC, leaf succulence, nocturnal acidification, and $\mathrm{ETR}_{\max}$. Tukey's post hoc tests were performed. Differences in SLA between species were analyzed with a nonparametric Kruskal–Wallis test followed by paired comparisons since this particular dataset did not fulfil the assumptions of the ANOVA (Kruskal & Wallis, 1952). Repeated measures ANOVA were performed using STATISTICA v.10 (Statsoft Inc., Tulsa, OK, USA); regressions and Kruskal–Wallis were run using the program SPSS 22 (Chicago, IL, USA). A value of $p < .05$ was used as the cut-off for significant differences.

Results

Environmental Conditions

During the transition from the early dry to the dry season, nocturnal relative humidity progressively decreased ($R^2 = .13$, $p = .02$ Figure 2(a)), while both nocturnal temperature ($R^2 = .53$, $p < .001$; Figure 2(b)) and vapor pressure deficit ($R^2 = .30$, $p < .01$; Figure 2(c)) increased.

Dew Deposition

Leaf temperature measurements indicate that the average dew deposition lasted 04:24 to 05:26 h every night in uncovered plants (Figure 3(a)), with a significant species effect, $F(3, 672) = 5.806$, $p < .001$. Dew duration was significantly longer in *T. elongata* compared with *T. yucatana* (Tukey's test, $p < .05$). The treatment effect was also significant, $F(1, 672) = 1047.1$, $p < .001$, as the covered plants had much shorter periods of dew deposition. Among covered plants, dew formation lasted only 00:20 to 01:02 h (Figure 3(a)) and species differences were not significant. The leaf wetness sensors gave similar results with an average of dew deposition duration of 08:01 h in the exposed, and 01:09 h for the covered treatments (Figure 3(b)). Leaf temperature showed a sharp decrease between 18:00 and 06:00 h, while dew point of the air showed a more gradual decrease in both treatments (Figure 4). Dew point of the air was lower within the plastic tarp of the covered treatment (Figure 4), which caused plants in this treatment to reach the dew point for much shorter periods.

Specific Leaf Area

Pairwise comparisons found species differences among in SLA (H [3, $N = 58$] $= 47.18$; $p < .001$; Table 1). *T. elongata* and *T. brachycaulos* had the highest values (99.5 and 106.3 $cm^2\ g^{-1}$, respectively), followed by *T. fasciculata* and *T. yucatana* that showed the lowest SLA values (48.4 and 36.2 $cm^{-2}\ g^{-1}$, respectively).

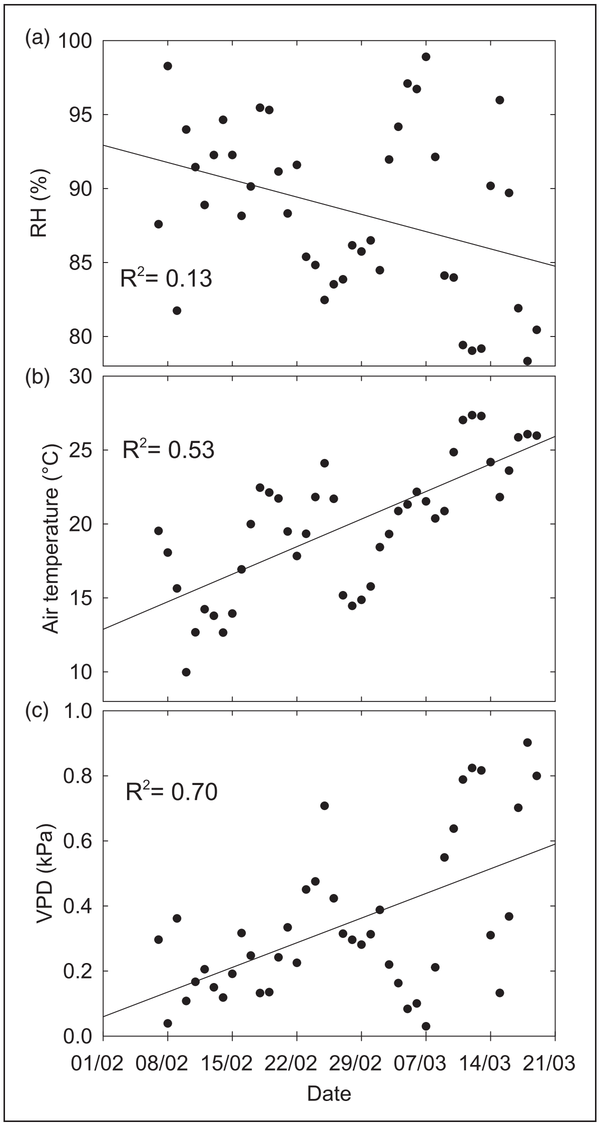

Figure 2. Change in average nocturnal (18:00 – 06:00) environmental conditions during the experiment. (a) Relative humidity, (b) air temperature, and (c) vapor pressure deficit (VPD). Solid lines represent significant linear regressions.

Water Relations

Progression of the dry season and the exposure to dew treatments affected the water relations of the four species differently (Figure 5). *T. yucatana* showed the largest drop in RWC between the early dry and dry season (mean decrease of 30% from its original values, Tukey $p < .05$; Figure 5(a) and (b)), but this species was not affected by the nightly covered treatment. *T. fasciculata* had the smallest reduction in RWC in both treatments (mean reduction of 8.5%; Figure 5(a) and (b)), and differences were non-significant; this species was not affected by treatment either. In the case of *T. elongata* and *T. brachycaulos*, reduction of RWC between early dry

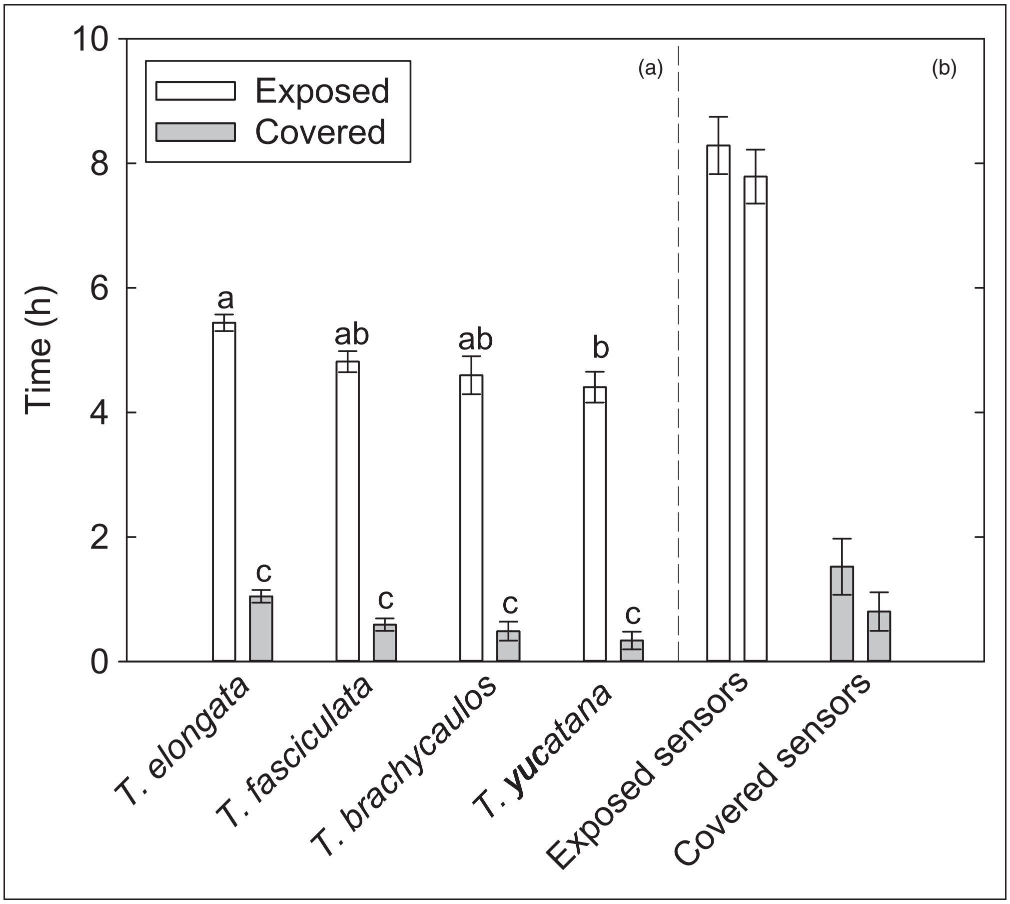

Figure 3. Duration of deposition as calculated for the leaves of exposed and covered plants (a), or registered by exposed and covered leaf wetness sensors adjacent to the plants (b). Data are means ± SE (*n* = 6–8). Different letters indicate significant differences.

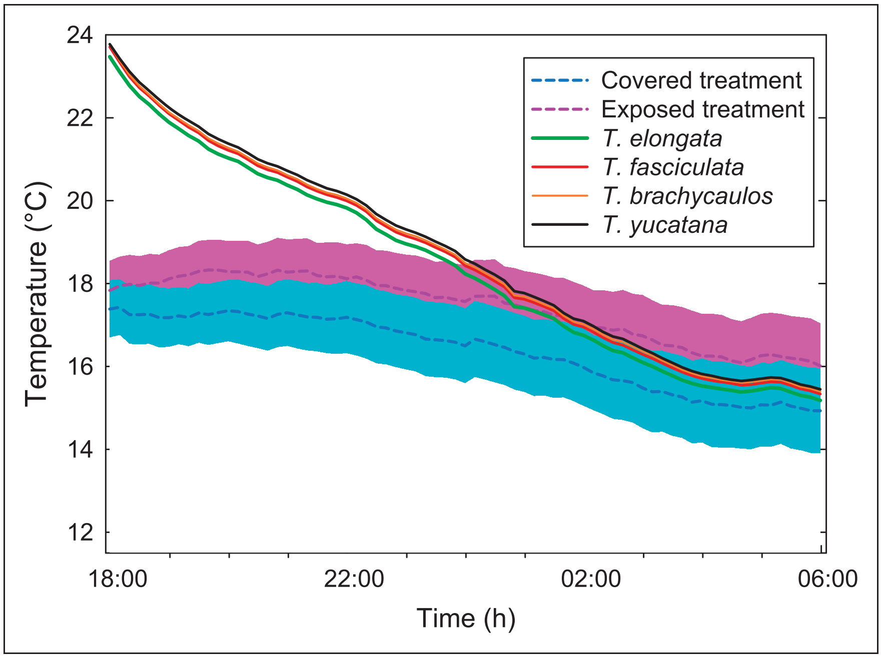

Figure 4. Time course of dew point of the air in the cover treatment and exposed control (dashed lines), and leaf temperature of *T. elongata*, *T. fasciculata*, *T. brachycaulos* and *T. yucatana* (solid lines), in the period from 07/02 to 19/03/2016. Data are means, shaded areas indicate ± *SE*.

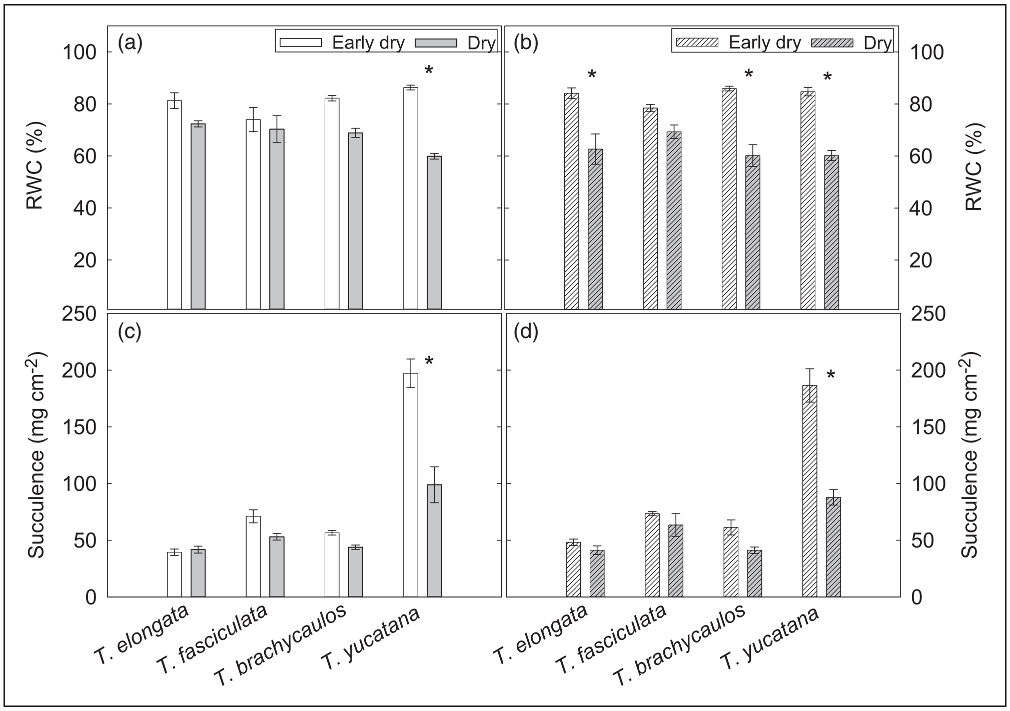

Figure 5. Water relations at the beginning (early dry season: All plants exposed to rain and dew) and at the end (dry season: half of the plants dew deprived) of the 8-week long experiment, for leaves of *T. elongata*, *T. fasciculata*, *T. brachycaulos*, and *T. yucatana* in the exposed (open bars) and covered treatments (shaded bars), (a) RWC for exposed plants, (b) RWC for covered plants, (c) leaf succulence for exposed plants, and (d) leaf succulence for covered plants. Data are means ± SE ($n = 6$–8). Asterisks indicate significant differences between seasons for each species and treatment. RWC = relative water content.

and dry season was only significant in covered plants (Tukey, $p < .05$), with a 26% and 30% decrease, respectively (Figure 5(b)), compared to the plants exposed to dew (5% and 11% decrease, respectively; $p > .05$, Figure 5(a)).

Overall, there were species differences in succulence, with *T. elongata* having the least succulent leaves (mean value of 43.8 mg H_2O cm^{-2} at the beginning of the experiment) and *T. yucatana* having the most succulent leaves (initially 191.8 mg H_2O cm^{-2}, $p < .001$). However, only *T. yucatana* showed significant changes in succulence, with a reduction of approximately 50% during of the dry season (Tukey $p < .0001$); in the overall ANOVA, there was a significant Species × Time interaction; $F(3, 50) = 47.15$, $p < .0001$. The other three species showed a nonsignificant tendency to lower succulence as the drought progressed. Covering did not affect succulence in any of the species significantly.

Carbon Metabolism

Overall, the species had differences in nocturnal acidification, with *T. fasciculata* and *T. brachycaulos* reaching higher values than *T. yucatana* (Tukey, species effect $p < .05$). With the onset of the dry season, there was a tendency toward reduced nocturnal carbon uptake (measured as tissue acidification) (Figure 6(a) and (b)), with different species responses to the nightly covered treatment, Time × Species × Treatment interaction, $F(3, 46) = 3.74$, $p < .05$. Nocturnal acidification in dew-deprived *T. brachycaulos* plants was reduced by >50% with the progressing dry season (Tukey $p < .05$). In comparison, exposed plants had a nonsignificant reduction of ~27%. *T. elongata* did not show significant changes but had the same tendency as *T. brachycaulos* with a larger decrease in acidification in covered than exposed plants. *T. fasciculata* showed the opposite trend with a significant reduction in tissue acidification (~47%, Tukey $p < .05$) only found in exposed plants, with no significant change in covered plants. *T. yucatana* showed no significant change related to season or treatment, although there was a large nonsignificant reduction in acidity (~50%) with the onset of the dry season.

Contrary to our expectations, there was a tendency to increase ETR_{max} values from the early dry to dry season (Figure 6(b) and (c)). However, this increase was significant only for *T. yucatana*, which also had the highest values at the end of the experiment, ~60% increase, Tukey $p < .01$, overall ANOVA significant Species × Time interaction; $F(3, 30) = 6.32$ $p < .0001$. The covered

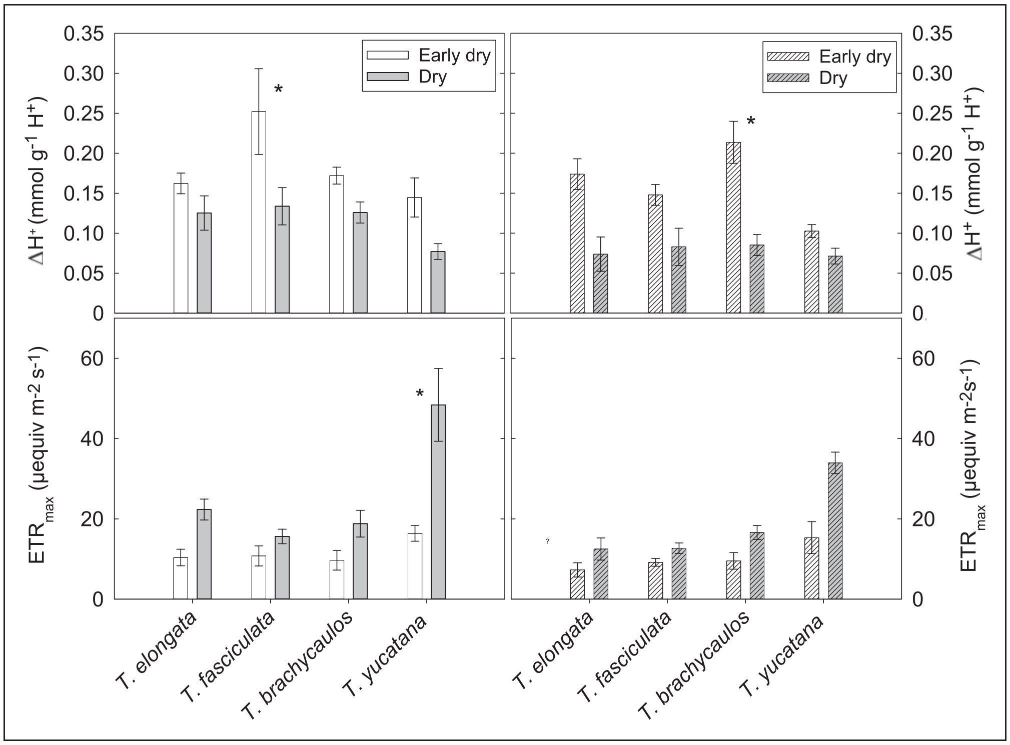

Figure 6. Nocturnal acidification (ΔH^+) and maximum electron transport rate (ETR_{max}) at the beginning (early dry season: All plants exposed to rain and dew) and at the end (dry season: half of the plants dew deprived) of the 8-week long experiment, for leaves of *T. elongata*, *T. fasciculata*, *T. brachycaulos*, and *T. yucatana* in the exposed (open bars) and covered treatments (shaded bars). (a) ΔH^+ for exposed plants, (b) ΔH^+ for covered plants, (c) ETR_{max} for exposed plants, and (d) ETR_{max} for covered plants. Data are means ± SE ($n = 6$–8 for ΔH^+, and $n = 5$ for ETR_{max}). Asterisks indicate significant differences between seasons for each species and treatment.

treatment did not have a significant effect on any of the species.

Discussion

As expected, during the transition from early dry to dry season, the canopy microenvironment showed a progressive nighttime increase in air temperature and decrease in air humidity (Figure 2). Despite the lack of rainfall, nighttime dew formation was consistently recorded for several hours both on the leaves of the epiphytic Bromeliaceae and on the leaf wetness sensors (Figures 3 and 4). There were, however, differences among bromeliad species in both the amount of dew condensed in its leaves and the influence of that water source on plant water status and carbon metabolism.

Our data evidence a gradient of dew formation among the species, with the leaves of *T. elongata* staying under the dew point of the air during a longer period every night, in comparison to the species with the shortest period, *T. yucatana* (Figures 3 and 4). In several ways, these two species represent contrasting morphological strategies, which may influence their capacity for dew condensation. The less succulent leaves of *T. elongata* lose more heat to the environment and thus get cooler (Andrade, 2003), promoting leaf temperature to drop below the dew point faster during the night. In contrast, *T. yucatana* had the most succulent leaves, which represent important water reserves for this species that is abundant at sites with very low annual rainfall (Cach-Pérez et al., 2013). The high thermal capacity of water means that the succulent leaves will take longer to cool during the night (Griffiths & Males, 2017), reducing dew deposition. Flat surfaces found in the wide leaves with horizontal angles of the tank species, *T. elongata*, also promote dew condensation (Kidron, 2005); while the tubular, twisted leaves of the atmospheric *T. yucatana* lack these surfaces. Leaf morphology also evidences that *T. elongata* has higher leaf surface per unit weight than *T. yucatana* (SLA; Table 1), again increasing the surface exposed for dew formation and absorption in the former species. Finally, the water absorbing leaf trichomes may obstruct dew formation, since water droplets form on the exposed cooler leaf cuticle (Pierce, 2007). Trichome size and density are variable among the *Tillandsia* species studied, with *T. elongata* having the lowest density and smaller trichome size and *T. yucatana* having higher density and larger trichomes (Cach-Pérez et al., 2016). Together, leaf succulence, shape, angle, and trichome cover contribute to longer dew condensation time in *T. elongata* and a shorter time in *T. yucatana*. the The other two *Tillandsia* species have intermediate values of these morphological variables and show intermediate duration of dew formation.

Experimental data have shown that fog (or dew) might not be enough to support growth or recover high RWC in epiphytic bromeliads from a tropical dry deciduous forest after a drought treatment (Reyes-García et al., 2012). However, we hypothesized that it could contribute to delay the effects of the dry season by maintaining favourable water status and allowing some carbon uptake. Our results support this hypothesis for those species with leaves showing longer hours below dew point. *T. elongata* and *T. brachycaulos* did not suffer significant water loss from the early dry to the dry season when exposed to dew but lowered their RWC 26% to 30% under the dew deprived treatment (Figure 5). The effect of the conserved water status was evident on carbon metabolism in *T. brachycaulos*, showing a consistent pattern of maintained nocturnal acidity values under dew–exposure, but reduced acidity when dew deprived (Figure 6). The same nonsignificant pattern was observed in *T. elongata*.

Overall, *T. fasciculata* seemed unaffected by the seasonal drought or the dew deprivation treatment; this species did not show changes in any of the water (Figure 5) or carbon use (Figure 6) parameters measured. *T. fasciculata* was the largest sized of the species used in this study (Table 1), and this confers more area to store water and in general a higher capacity to withstand stress (Zotz, Hietz, & Schmidt, 2001). Its thick leaves (SLA; Table 1) provide a lower ratio of plant leaf area to plant water content, allowing the species to maintain stomata open during the drought, but with a relatively low loss in internal water content (Zotz & Andrade, 1998). The high nocturnal acidification observed (Figure 6) could also be related to high water use efficiency in this species. Thus, a more intense or longer drought would be needed to evaluate whether dew is being used by *T. fasciculata*.

The unexpected increase in ETR_{max} during the experiment in all species (Figure 6) partly reflects an increase in incident light as the trees begin to lose their leaves in response to drought, increasing approximately 30% (from 14 to 21 mol m^{-2} d^{-1}, data not shown). Yet, the increase in ETR was unaccompanied by a similar increase in carbon uptake measured as nocturnal acid accumulation; this phenomenon, observed in bromeliads, has been assumed to reflect photorespiration and to be important for photoprotection (Maxwell, 2002; Rosado-Calderón et al., 2018). This excess (presumably photorespiratory) ETR has been shown to be higher in phenotypes previously adapted to drier conditions than those grown under milder environments (Rosado-Calderón et al., 2018). The high ETR shown in *T. yucatana* may relate to its success in the driest sites of the peninsula, such as mangroves and coastal scrubs (Cach-Pérez et al., 2013), where the need to dissipate excess energy may be large.

In summary, while nocturnal dew can be an important source of water for epiphytic bromeliads in the deciduous forest of Dzibilchaltún during the transition from the early dry to the dry season, its importance varies among species, and the access to this secondary water source may depend on morphology.

Implications for Conservation

Epiphytes are highly sensitive to changes in the environment, this makes them particularly vulnerable to climate change (Cach-Pérez, Andrade, & Reyes-García, 2014; Wagner & Zotz, 2018), which also makes them possible early indicators of the effects of climate change on forests (Cach-Pérez et al., 2014, 2018). Since the formation of dew is closely related to the minimum daily temperature, increasing temperatures as a consequence of climate change may negatively affect its availability in the future. In the case of the Yucatán Peninsula, more intense dry seasons and higher temperatures are expected to be more frequent with climate change (Orellana, Espadas, Conde, & Gay, 2009). Changes in the dew deposition regime could be followed by monitoring yearly changes in the RWC during the early dry season, especially in species like *T. brachycaulos* and *T. elongata*. Here, we show that while dew may not be a source of water as important as rain, it is still a valuable one and its scarcity may have a negative effect on the survival of sensitive species.

Acknowledgments

The authors thank Roberth Us, Celene Espadas, Manuela Tamayo, Susana Dzib, and Harry Moreno for field and laboratory assistance. The authors also thank Dzibilchaltún National Park-INAH.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: Eduardo Chávez-Sahagún received a scholarship from CONACYT 419242, the study was funded by SEP-

CONACYT project 221490 and INEGI-CONACYT project 290916.

ORCID iD

Eduardo Chávez-Sahagún https://orcid.org/0000-0002-9496-2897
Casandra Reyes-García https://orcid.org/0000-0001-9847-9053

References

Andrade, J. L. (2003). Dew deposition on epiphytic bromeliad leaves: An important event in a Mexican tropical dry deciduous forest. *Journal of Tropical Ecology*, *19*(5), 479–488.

Bader, M. Y., Menke, G., & Zotz, G. (2009). Pronounced drought tolerance characterizes the early life stages of the epiphytic bromeliad *Tillandsia flexuosa*. *Functional Ecology*, *23*, 472–479.

Benzing, D. H. (1990). *Vascular epiphytes. General biology and related biota* (1st ed.). Cambridge, England: Cambridge University Press.

Benzing, D. H. (2000). *Bromeliaceae: Profile of an adaptative radiation*. Cambridge, England: Cambridge University Press.

Benzing, D. H., Henderson, K., Kessel, B., & Sulak, J. (1976). The absorptive capacities of bromeliad trichomes. *American Journal of Botany*, *63*(7), 1009–1014.

Cach-Pérez, M. J., Andrade, J. L., Cetzal-Ix, W., & Reyes-García, C. (2016). Environmental influence on inter and intraspecific variation in density and morphology of stomata and trichomes of epiphytic bromeliads of the Yucatan Peninsula. *Botanical Journal of the Linnean Society*, *181*, 441–458.

Cach-Pérez, M. J., Andrade, J. L., Chilpa-Galván, N., Tamayo-Chim, M., Orellana, R., & Reyes-García, C. (2013). Climatic and structural factors influencing epiphytic bromeliad community assemblage along a gradient of water-limited environments in the Yucatan. *Tropical Conservation Science*, *6*(1), 283–302.

Cach-Pérez, M. J., Andrade, J. L., & Reyes-García, C. (2014). La susceptibilidad de las bromeliáceas epífitas al cambio climático [Susceptibility of epiphytic bromeliads to climate change]. *Botanical Sciences*, *92*(2), 157–168.

Cach-Pérez, M. J., Andrade, J. L., & Reyes-García, C. (2018). Morphophysiological plasticity in epiphytic bromeliads across a precipitation gradient in the Yucatan peninsula, Mexico. *Tropical Conservation Science*, *11*, 1–10.

Cavelier, J., & Goldstein, G. (1989). Mist and fog interception in elfin cloud forests in Colombia and Venezuela. *Journal of Tropical Ecology*, *5*(3), 309–322.

Chilpa-Galván, N., Tamayo-Chim, M., Andrade, J. L., & Reyes-García, C. (2013). Water table depth may influence the asymmetric arrangement of epiphytic bromeliads in a tropical dry forest. *Plant Ecology*, *214*(8), 1037–1048.

Crayn, D. M., Winter, K., & Smith, J. A. C. (2004). Multiple origins of crassulacean acid metabolism and the epiphytic habit in the Neotropical family Bromeliaceae. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(10), 3703–3708.

Dodd, A. N., Borland, A. M., Haslam, R. P., Griffiths, H., & Maxwell, K. (2002). Crassulacean acid metabolism: Plastic, fantastic. *Journal of Experimental Botany*, *53*(369), 569–580.

Givnish, T. J., Barfuss, M. H. J., Ee, B., Van, Riina, R., Schulte, K., Horres, R., . . . Ytsma, K. J. (2014). Adaptive radiation, correlated and contingent evolution, and net species diversification in Bromeliaceae. *Molecular Phylogenetics and Evolution*, *71*(1), 55–78.

González, A. L., Fariña, J. M., Pinto, R., Pérez, C., Weathers, K. C., Armesto, J. J., & Marquet, P. A. (2011). Bromeliad growth and stoichiometry: Responses to atmospheric nutrient supply in fog-dependent ecosystems of the hyper-arid Atacama Desert, Chile. *Oecologia*, *167*, 835–845.

Graham, E. A., & Andrade, J. L. (2004). Drought tolerance associated with vertical stratification of two co-occurring epiphytic bromeliads in a tropical dry forest. *American Journal of Botany*, *91*(5), 699–706.

Griffiths, H., & Males, J. (2017). Succulent plants. *Current Biology*, *27*(17), R890–R896.

Guevara-Escobar, A., Cervantes-Jiménez, M., Suzán-Azpiri, H., González-Sosa, E., Hernández-Sandoval, L., Malda-Barrera, G., & Martínez-Díaz, M. (2011). Fog interception by Ball moss (*Tillandsia recurvata*). *Hydrology and Earth System Sciences*, *15*(8), 2509–2518.

Herrera-Silveira, J. A. (1995). Seasonal patterns and behavior of nutrients in a tropical coastal lagoon with groundwater discharges. *Journal of Ecology and Environmental Science*, *22*(1), 45–57.

Jones, H. G. (1992). *Plants and microclimate: a quantitative approach to environmental plant physiology* (2nd ed.). Cambridge: Cambridge University Press.

Kidron, G. J. (2005). Angle and aspect dependent dew and fog precipitation in the Negev desert. *Journal of Hydrology*, *301*(1), 66–74.

Kruskal, H. W., & Wallis, W. A. (1952). Use of ranks in one-criterion variance analysis. *Journal of the American Statistical Association*, *47*(260), 583–621.

Lawrence, M. G. (2005). The relationship between relative humidity and the dewpoint temperature in moist air: A simple conversion and applications. *Bulletin of the American Meteorological Society, 86*(2), 225–233.

Lüttge, U. (1989). *Vascular plants as epiphytes* (*vol. 53*). Berlin, Germany: Springer-Verlag.

Martin, C. E. (1994). Physiological ecology of the Bromeliaceae. *The Botanical Review*, *60*(1), 1–82.

Martorell, C., & Ezcurra, E. (2007). The narrow-leaf syndrome: A functional and evolutionary approach to the form of fog-harvesting rosette plants. *Oecologia*, *151*(4), 561–573.

Maxwell, K. (2002). Resistance is useful: Diurnal patterns of photosynthesis in C_3 and crassulacean acid metabolism epiphytic bromeliads. *Functional Plant Biology*, *29*(6), 679–687.

Maxwell, K., & Johnson, G. N. (2000). Chlorophyll fluorescence – a practical guide. *Journal of Experimental Botany, 51*(345), 659–668.

Nobel, P. S. (2009). *Physicochemical and environmental plant physiology* (4th ed.). Cambridge, MA: Academic Press.

North, G. B., Lynch, F. H., Maharaj, F. D. R., Phillips, C. A., & Woodside, W. T. (2013). Leaf hydraulic conductance for a tank bromeliad: Axial and radial pathways for moving and conserving water. *Frontiers in Plant Science*, *4*(4), 1–10.

Orellana, R. (1999). Evaluación climática. In A. García & J. Córdoba (Eds.), *Atlas de procesos territoriales de Yucatán* [Climatic evaluation. In A. Garcia & J. Cordoba (Eds.), Atlas of territorial processes of Yucatán] (pp. 163–182). Mérida, Yucatán: Universidad Autónoma de Yucatán.

Orellana, R., Espadas, C., Conde, C., & Gay, C. (2009). *Atlas. Escenarios de cambio climático en la Península de Yucatán* [Atlas of Climate Change Scenarios in the Yucatan Peninsula] (1st ed.). Mexico: Centro de Investigación Científica de Yucatán, AC.

Pierce, S. (2007). The jeweled armor of Tillandsia—Multifaceted or elongated trichomes provide photoprotection. *Aliso: A Journal of Systematic and Evolutionary Botany*, *23*(1), 44–52.

Pinto, R., Barría, I., & Marquet, P. A. (2006). Geographical distribution of *Tillandsia* lomas in the Atacama Desert, northern Chile. *Journal of Arid Environments*, *65*(4), 543–552.

Pittendrigh, C. S. (1948). The bromeliad–anopheles–malaria complex in Trinidad. I-The bromeliad flora. *Evolution*, *2*(1), 58–89.

Ramirez-Morillo, I. M., Carnevali, F. C. G., & Chi May, F. (2004). *Guía ilustrada de las Bromeliaceae de la porción mexicana de la Península de Yucatán* (1st ed.). [Ilustrated guide of the Bromeliaceae from the mexican portion of the Yucatán peninsula (1st ed.).] Mérida, Yucatán: Centro de Investigación Científica de Yucatán AC.

Rapp, J. M., & Silman, M. R. (2014). Epiphyte response to drought and experimental warming. *F1000Research*, *7*, 1–25.

Reyes-García, C., Griffiths, H., Rincón, E., & Huante, P. (2008). Niche differentiation in tank and atmospheric epiphytic bromeliads of a seasonally dry forest. *Biotropica*, *40*(2), 168–175.

Reyes-García, C., Mejia-Chang, M., & Griffiths, H. (2012). High but not dry: Diverse epiphytic bromeliad adaptations to exposure within a seasonally dry tropical forest community. *New Phytologist*, *193*, 745–754.

Rosado-Calderón, A. T., Tamayo-Chim, M., de la Barrera, E., Ramírez-Morillo, I. M., Andrade, J. L., Briones, O., & Reyes-García, C. (2018). High resilience to extreme climatic changes in the CAM epiphyte *Tillandsia utriculata* L. (Bromeliaceae). Physiologia Plantarum, 1–16.

Thien, L. B., Bradburn, A. S., & Welden, A. L. (1982). The woody vegetation of Dzibilchaltún. A maya archeological site in Northwest Yucatán, México. *Middle American Research Institute Occasional Papers*, *5*, 1–24.

Wagner, K., & Zotz, G. (2018). Epiphytic bromeliads in a changing world: The effect of elevated CO_2 and varying water supply on growth and nutrient relations. *Plant Biology*, *20*(3), 636–640.

Wolf, J. H. D., & Alejandro, F. S. (2003). Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *Journal of Biogeography*, *30*, 1689–1707.

Wu, Y., Song, L., Liu, W., Liu, W., Li, S., Fu, P., . . . Lu, H. (2018). Fog water is important in maintaining the water budgets of vascular epiphytes in an Asian Tropical Karst Forests during the dry season. *Forests*, *9*(5), 1–14.

Zotz, G. (2013). The systematic distribution of vascular epiphytes-a critical update. *Botanical Journal of the Linnean Society*, *171*(3), 453–481.

Zotz, G., & Andrade, J. L. (1998). Water relations of two co-occurring epiphytic bromeliads. *Journal of Plant Physiology*, *152*(4-5), 545–554.

Zotz, G., & Hietz, P. (2001). The physiological ecology of vascular epiphytes: Current knowledge, open questions. *Journal of Experimental Botany*, *52*(364), 2067–2078.

Zotz, G., Hietz, P., & Schmidt, G. (2001). Small plants, large plants: The importance of plant size for the physiological ecology of vascular epiphytes. *Journal of Experimental Botany*, *52*(363), 2051–2056.

Zotz, G., & Thomas, V. (1999). How much water is in the tank? Model calculations for two epiphytic bromeliads. *Annals of Botany*, *83*, 183–192.