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HOT BUT NOT DRY: MODEST CHANGES IN WATER RELATIONS FOR AN EPIPHYTIC BROMELIAD IN A TROPICAL DRY DECIDUOUS FOREST

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Premise of research. Epiphytic bromeliads endure intense seasonal environmental changes in the canopy of dry tropical deciduous forests. The analysis of the physiological responses of these epiphytes to environmental changes can be useful in assessing their plasticity, vulnerability, and adaptations to such extreme habitats.

Methodology. We measured microenvironmental variables and water relations for plants of the epiphytic bromeliad *Tillandsia brachycaulos* in three microhabitats within the canopy of a dry tropical forest. We measured individual plants for seasonal and spatial differences in light, leaf temperature, osmotic potential, cell wall elasticity, and relative capacitance as indications of their physiological responses to the changing environment.

Pivotal results. We detected greater physiological differences for leaves of *T. brachycaulos* among seasons than among microhabitats. Osmotic potential decreased in the early dry season, especially in the low and middle strata within the canopy, and leaf relative capacitance increased.

Conclusions. Individuals of *T. brachycaulos* displayed modest leaf physiological responses to the strong seasonal environmental changes within the canopy of this tropical forest. Such responses are in agreement with the observation that when water is available, it has high water potential, and thus water storage is the main strategy for surviving in such extreme conditions.

Keywords: leaf temperature, osmotic potential, relative capacitance, *Tillandsia brachycaulos*, Yucatán.

Introduction

Vertical stratification of epiphytes is well documented in tropical forests (Rascher et al. 2012; Wagner et al. 2013; Petter et al. 2016). In tropical dry deciduous forests, seasonal rainfall and deciduousness can dramatically change the environmental conditions for epiphytes. For example, incident photosynthetic photon flux (PPF; μmol m^{-2} s^{-1}) for some epiphytes is about nine times higher during the dry season than during the wet season (Graham and Andrade 2004; Cervantes et al. 2005). Moreover, during the warmest times of the day, the leaf temperatures of plants in lower sites within the canopy are significantly higher than the temperature of the air, which can affect growth and reproduction (Cervantes et al. 2005). To cope with these strong seasonal changes in microenvironment, epiphytes possess several adaptations, such as succulence, water-impounding shoots, specialized roots, crassulacean acid metabolism (CAM), and foliar trichomes (Benzing 1990; Zotz 2016). Indeed, epiphyte position in the canopy often depends on a combination of these characteristics and on the ability to acclimate to environmental changes (Maxwell et al. 1995; Andrade and Nobel 1997; Hietz and Briones 1998; Zotz and Andrade 1998; Griffiths and Maxwell 1999; Gonzalez-Salvatierra et al. 2010; Cach-Pérez et al. 2013; Chilpa-Galván et al. 2013; de la Rosa-Manzano et al. 2017).

In tropical dry deciduous forests, changes in water availability with season can be extreme. During the dry season, the decreased water availability for epiphytes is accompanied by an increase of PPF due to the deciduousness of the host trees, further enhancing desiccating conditions and increasing stress (Graham and Andrade 2004; Reyes-García et al. 2012; Crain and Tremblay 2017). This increase in light is usually accompanied by increases in temperature and vapor pressure deficit (VPD), which explains the prevalence of CAM species in tropical dry ecosystems (Griffiths and Smith 1983; Cervera et al.

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2006; Reyes-García et al. 2008; Ricalde et al. 2010; Cach-Pérez et al. 2013).

Although succulence recovery is very rapid in epiphytes and occurs within a few hours or a few days after rewetting (Sinclair 1983; Andrade and Nobel 1997), neither water tissue recovery nor CAM can fully explain the occurrence of an epiphyte in a particular microsite within the canopy. For epiphytic orchids, leaf area, leaf size, leaf succulence, and pseudobulb size are important for survival in certain microsites in tropical dry forests (de la Rosa-Manzano et al. 2014*a*, 2014*b*). In other forests, different adaptive mechanisms as a response to drought (either escape or avoidance) may be predominant within specific microhabitats (Zhang et al. 2016). Interestingly, individuals in exposed positions in the canopy may have more access to dew or fog, reducing drought stress under such potentially more extreme conditions (Andrade 2003; Graham and Andrade 2004; Reyes-García et al. 2008; de la Rosa-Manzano et al. 2014*a*; Wu et al. 2018; Chávez-Sahagún et al. 2019). Exposure may also be associated with an increase in tissue relative capacitance compared with individuals in the shade (Andrade et al. 2009).

High tissue relative capacitance is the ability to maintain high water potentials when water content decreases, and it relates to succulence, the tissue volume–to–surface area ratio, osmotic adjustment, and the volumetric elastic modulus (ϵ; Nobel 2009; Jones 2013). Even though epiphytes tend to be drought tolerant, osmotic potentials (Ψ_π) are unexpectedly high and are regularly less negative than -1.0 MPa (Sinclair 1983; Smith et al. 1986; Martin 1994; Zotz and Hietz 2001; Martin et al. 2004; de la Rosa-Manzano et al. 2014*b*). However, some epiphytic bromeliads decrease Ψ_π to about -1.5 MPa during the dry season (Cach-Pérez et al. 2018).

Individuals of the epiphyte *Tillandsia brachycaulos* Schlechtendal (Bromeliaceae) are abundant in tropical dry deciduous forests of northern Yucatán, Mexico, and they occur nearly everywhere in the host trees, from very close to the forest floor to the upper canopy (Mondragón et al. 1999). A previous study indicated that those individuals inhabiting the lower canopy have reduced growth and reproduction rates, which are also correlated with high leaf temperatures (Cervantes et al. 2005). However, water relations studies for this species in different vertical microhabitats are lacking. We hypothesized that plants of *T. brachycaulos* would increase their foliar relative capacitance in the dry season, mainly through a decrease of Ψ_π. Those plants growing in the lower canopy were expected to enhance their relative capacitance more than individuals in the upper canopy, which would have more access to rain, fog, and dew, all water sources at high water potential (Andrade 2003; Graham and Andrade 2004; Reyes-García et al. 2012).

Material and Methods

Study Site and Plant Species

Field measurements were made in Dzibilchaltún National Park, a secondary tropical dry deciduous forest regenerating in a 539-ha protected area (lat. 21°05′N, long. 89°35′W; 10 m in elevation) in the Yucatán Peninsula, Mexico. Trees in the family Fabaceae dominate the forest. It receives 650–700 mm in annual rainfall and has a mean air temperature of 26°C, a maximum of 45°C, and a minimum of 10°C (Thien et al. 1982). Most trees are leafless during the dry season, which occurs from March to May. Between the wet and dry seasons there is an early dry season, locally known as "nortes" (from November to February), characterized by 2- to 3-d events of strong winds (>80 km h^{-1}), little rainfall (20–60 mm), and relatively low temperatures (<20°C; Orellana 1999).

Tillandsia brachycaulos is one of the most abundant and widespread epiphytic bromeliads in the Yucatán Peninsula (Cach-Pérez et al. 2013). It is considered an atmospheric epiphyte (ecophysiological type V, according to Benzing [2000]), although it has some water impoundment capacity (Andrade 2003). Individuals of *T. brachycaulos* located in five neighboring trees of three species (*Gymnopodium floribundum* Rolfe, three individuals; *Pithecellobium dulce* (Roxb.) Benth; and *Randia obcordata* S. Watson) were selected for microenvironmental and physiological measurements. All tree species in the study site are of short stature (average height, 4.1 ± 0.3 m; Graham and Andrade 2004). Following previous studies (Cervantes et al. 2005; Chilpa-Galván et al. 2013), all measurements were performed on individuals from three canopy strata: from 0.30 to 0.40 m in height (low stratum), from 1.40 to 1.50 m in height (middle stratum), and from 2.50 to 2.60 m in height (high stratum). All adult plants in each stratum were labeled and mapped for random sampling.

Environmental Measurements

Because each season in the region is relatively well defined (Orellana 1999; Orellana et al. 2009), we chose to measure environmental variables for only three to five consecutive days within each season. PPF was measured at about 20 mm above randomly selected epiphytes ($n = 5$ per stratum) using gallium-arsenide-phosphide photodiodes (Hamamatsu, Middlesex, NJ) calibrated against an LI-190SB quantum sensor (LI-COR, Lincoln, NV). As a reference for PPF above the canopy, two additional sensors were placed at approximately 15 m above the ground in a clearing. Leaf temperatures were measured on the abaxial surface of one leaf per plant from midrosette using 0.08-mm-diameter copper-constantan thermocouples attached with porous adhesive tape. Air temperature and humidity were measured with a Vaisala shielded probe (HMP35C-L, Campbell Scientific, Logan, UT). All sensors 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).

Tissue Water Relations Measurements

Whole midrosette leaves of randomly selected individuals from each stratum were collected at 0700, 1300, and 1600 hours during 1 d in each season (first Monday of January, May, and August 2013; $n = 3$–5 per stratum); samples for Ψ_π were stored in liquid nitrogen and transported to the laboratory (within a 15-min drive). After thawing, leaf samples were crushed with a vice, and a filter-paper disk was saturated with the expressed cell sap. The saturated paper disk was then placed in a vapor pressure 5520 osmometer (Wescor, Logan, UT) to determine

Table 1

Daily Integrals of Photosynthetic Photon Flux (PPF), Maximum PPF, and Maximum Vapor Pressure Deficit (VPD) above the Canopy in Three Seasons in the Tropical Dry Deciduous Forest in Dzibilchaltún National Park

Season	Daily PPF (mol m^{-2} d^{-1})	Maximum PPF (μmol m^{-2} d^{-1})	Maximum VPD (kPa)
Early dry	40.9 ± 1.4	1928 ± 133	3.92 ± .32
Dry	46.4 ± 2.5	2400 ± 116	4.79 ± .76
Wet	39.5 ± 3.6	2060 ± 140	1.89 ± 1.63

Note. Data are means ± standard errors (n = 5).

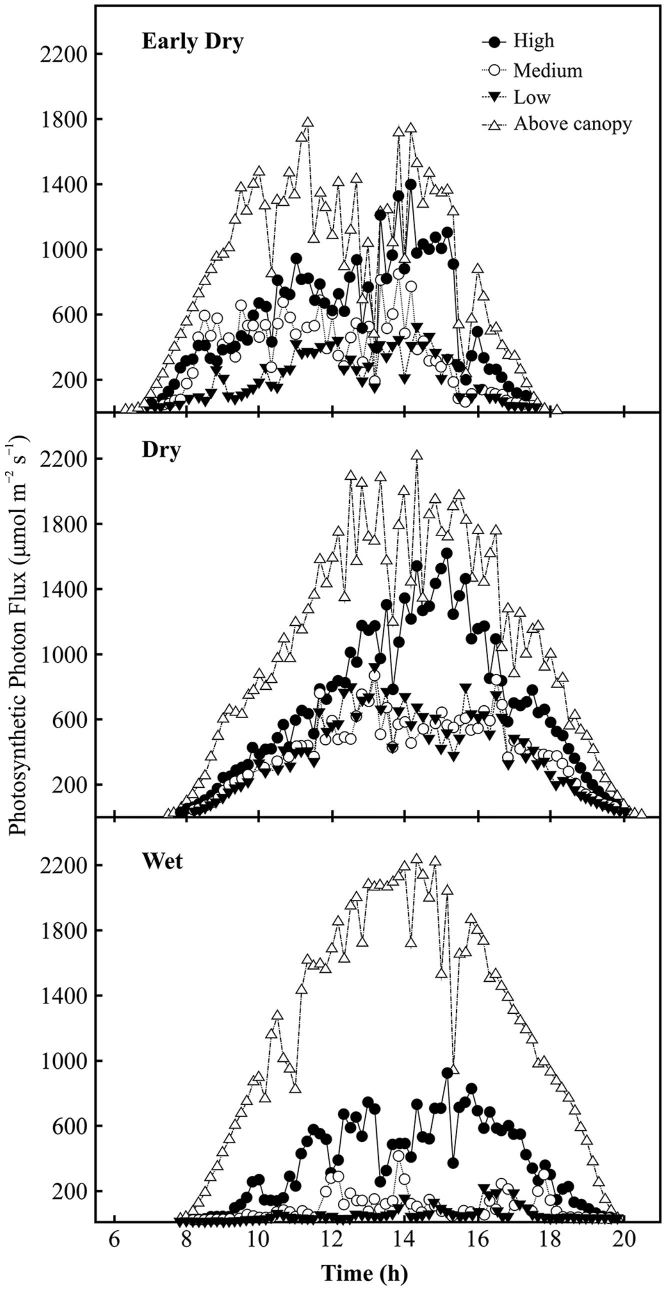

Fig. 1 Representative daily course of photosynthetic photon flux (PPF) above individuals of *Tillandsia brachycaulos* (n = 4) from different canopy strata (high strata represented by filled circles; medium represented by open circles; low represented by filled triangles) in the dry deciduous tropical forest of Dzibilchaltún National Park. PPF above the canopy (open triangles) is also shown. Measurements were taken on clear days during the early dry, dry, and wet seasons.

Table 2

Daily Integrals of Photosynthetic Photon Flux (PPF) above Individuals of *Tillandsia brachycaulos* at Three Strata within the Canopy and in Three Seasons in the Tropical Dry Deciduous Forest in Dzibilchaltún National Park

Stratum	Early dry season daily PPF (mol m^{-2} d^{-1})	Dry season daily PPF (mol m^{-2} d^{-1})	Wet season daily PPF (mol m^{-2} d^{-1})
Low	8.04 ± 1.41	17.39 ± 1.63	2.17 ± .32
Middle	13.58 ± 1.52	17.28 ± 2.06	3.37 ± .76
High	21.95 ± 3.69	31.43 ± 5.54	15.43 ± 6.63

Note. Data are means ± standard errors ($n = 5$).

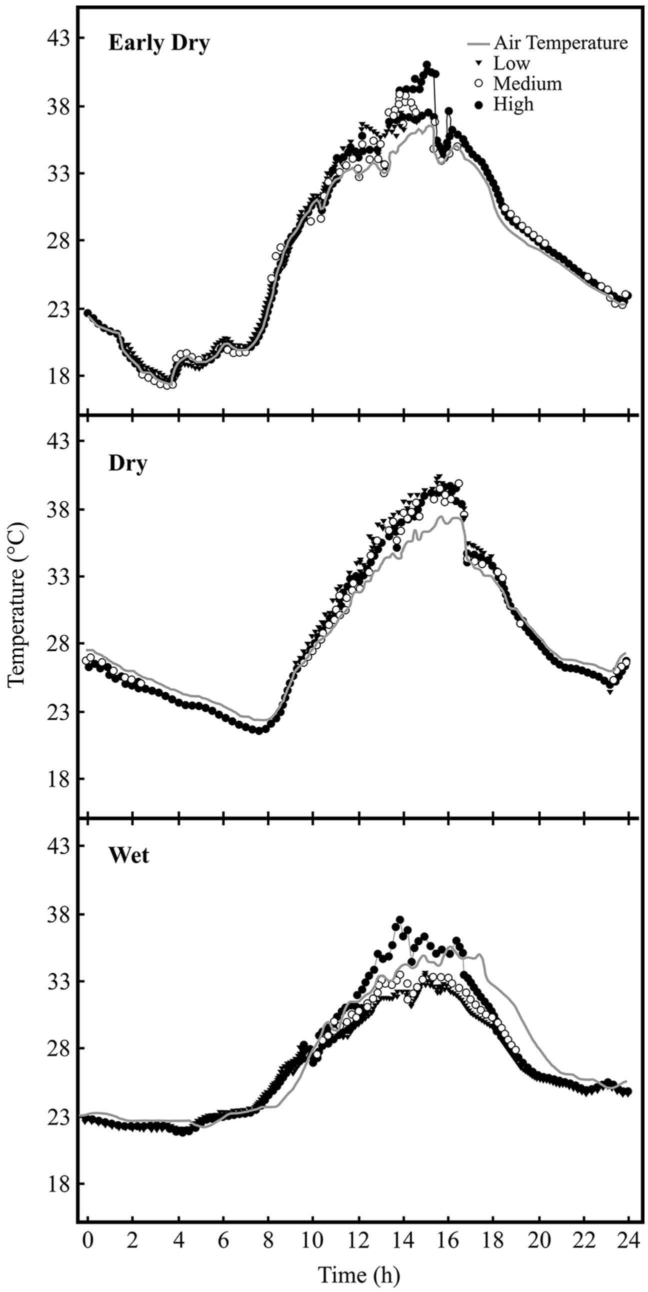

Fig. 2 Representative daily course of air temperatures (line) and leaf temperatures (symbols) of *Tillandsia brachycaulos* ($n = 4$) from different canopy strata (high strata represented by filled circles; medium represented by open circles; low represented by filled triangles) in the dry deciduous tropical forest of Dzibilchaltún National Park. Measurements were taken on clear days during the early dry, dry, and wet seasons.

osmolality (mmol/kg). Results were then converted to Ψ_π (MPa) using the van't Hoff relation (Nobel 2009).

Relative water content (RWC), defined as (fresh mass − dry mass)/(turgid mass − dry mass), was obtained for circular tissue samples (0.95 cm^2) from midrosette leaves. Turgid mass was obtained after the samples were hydrated for 6 h at 25°C in sealed plastic vials containing wet filter paper saturated with distilled water. Dry mass was obtained after the samples were dried at 60°C until no further weight change occurred (generally less than 24 h).

Water potential (Ψ_w) isotherms for leaf tissues were obtained psychometrically (Andrade and Nobel 1997; Zotz and Andrade 1998; Andrade et al. 2009). Fresh leaf tissue samples (5 mm in diameter) were hydrated as described above to reach an RWC of 1.0. We then placed hydrated samples in a vapor pressure osmometer (Wescor) to measure osmolality using the autorepeat mode. We then calculated Ψ_w as we had Ψ_π for the samples. Subsequent measurements of fresh mass and Ψ_w were performed repeatedly after samples were allowed to dry in the air for 5 min in ambient laboratory conditions. Dry mass was obtained as described above. The relative capacitance (change in RWC per unit change in Ψ_w) of the leaf tissues for an RWC between 1.0 and 0.6 was obtained from the water potential isotherms (the slope of each linear regression; n = 3–4 plants for each stratum). Previous studies indicate that the average RWC for *T. brachycaulos* does not decrease below 0.6 during the dry season (Cach-Pérez 2013). Similarly, ϵ of the leaf tissues was calculated from the water potential isotherms as the change in pressure potential (Ψ_p) for a unit change in RWC (Ogburn and Edwards 2012).

Statistical Analysis

ANOVA followed by Tukey's mean comparison tests was performed to evaluate differences in water relations. Three-way ANOVAs were done for the osmotic potential data; the factors were time of day, stratum, and season. In addition, osmotic data for plants in all locations within the canopy were evaluated against the season. A linear regression was applied to determine the relative capacitance. For relative capacitance and the volumetric elastic modulus, the factors were stratum and season. All statistical analyses were completed using the software Statistica 7.0 (StatSoft, Tulsa, OK).

Results

Microenvironmental Conditions

PPF and VPD above the canopy changed greatly during the year. During the early dry season, VPD increased relative to the wet season, and it reached the highest values during the dry season; maximum VPD values were 3.92 kPa in the early dry season and 4.79 kPa in the dry season (table 1). Maximum PPF above the canopy was the highest in the dry season (2400 ± 216 μmol m^{-2} s^{-1}; table 1).

Incident PPF above *Tillandsia brachycaulos* plants within the canopy also changed greatly during the year (fig. 1). During the afternoon in the early dry and dry seasons, individuals of *T. brachycaulos* in the high stratum had an incident PPF similar to the PPF above the canopy, but in the wet season, when host trees were fully leafed, PPF was lower than it was above the canopy for most individuals (fig. 1). In the dry season after host trees had dropped most of their leaves, the average daily PPF above *T. brachycaulos* in the high stratum was 31.43 ± 5.54 mol m^{-2} d^{-1}, almost two times greater than the incident PPF of individuals in the lower stratum ($P < 0.05$; table 2). During the wet season, the average daily PPF above *T. brachycaulos* at the high stratum was 15.43 ± 6.63 mol m^{-2} d^{-1}, about seven times greater than that of individuals in the low stratum ($P < 0.01$; table 2).

Temperature differences between the air and the leaves of *T. brachycaulos* during typical clear days had distinct seasonal differences (fig. 2). Leaf temperatures were higher than air temperatures during the daytime in the early dry and dry seasons, whereas in the wet season during the daytime, leaf temperatures of most individuals were lower than that of the air. At night, leaf temperatures were lower than the air temperature, mainly during the dry and wet seasons (fig. 2).

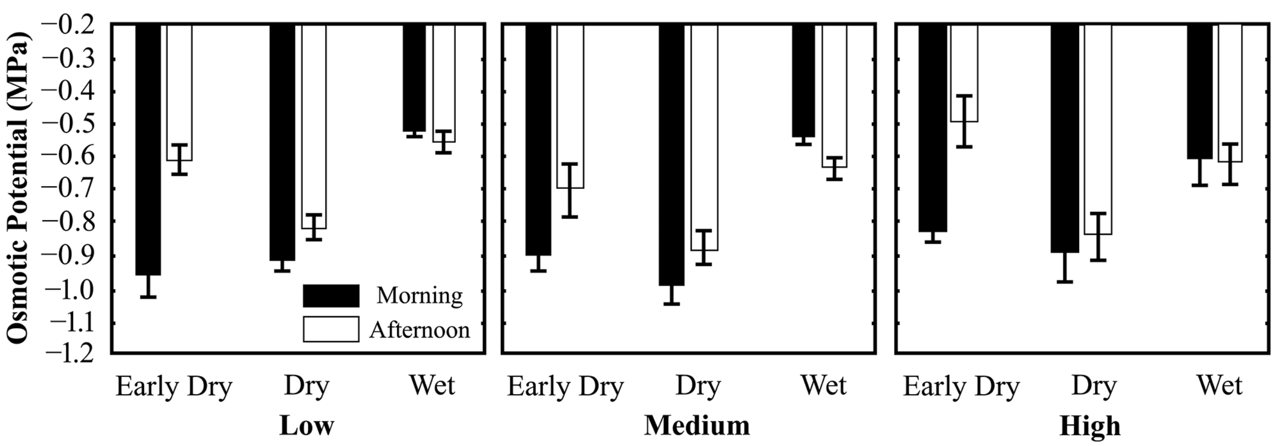

Fig. 3 Osmotic potentials of leaves of *Tillandsia brachycaulos* at two times of the day in three seasons and from different canopy strata in the dry deciduous tropical forest of Dzibilchaltún National Park. Data are means ± standard errors (n = 5).

Table 3

Osmotic Potential (Ψ_π) and Water Potential (Ψ_w) for Leaves of *Tillandsia brachycaulos* at Three Sampling Times during the Day for Data of all Seasons in the Tropical Dry Deciduous Forest in Dzibilchaltún National Park

	Morning (MPa)	Midday (MPa)	Afternoon (MPa)
Osmotic potential	−.79 ± .03*	−.74 ± .02	−.68 ± .02
Water potential	−.68 ± .03	−.66 ± .03	−.65 ± .04

Note. Data are means ± standard errors ($n = 45$).
* Significantly different (Tukey, $P < 0.05$).

Tissue Water Relations

Osmotic potential changed during the year for leaf tissues of *T. brachycaulos* (Ψ; fig. 3). Values of Ψ_π were lower in the morning compared with the midday and afternoon, independent of the season ($P < 0.05$; table 3). During the early dry and dry seasons, morning Ψ_π values were lower than during the wet season (fig. 3). Combined Ψ_π values for all strata were lowest in the dry season, higher in the early dry season, and highest in the wet season ($F_{2,42} = 4.05$, $P < 0.05$; fig. 4).

In the early dry and wet seasons, leaf relative capacitance was significantly different between the low and middle strata (fig. 5 for the early dry season only; $P < 0.05$). In the wet season, epiphytes in the high stratum had a high variation in leaf relative capacitance, and no differences in leaf relative capacitance occurred among strata in the dry season (fig. 6).

The volumetric elastic modulus of the leaf samples varied over a range of 4.3 MPa, with the lowest value occurring for leaves in the high stratum during the dry season, indicating a relatively higher cell wall elasticity (table 4). The highest value for ϵ occurred for leaves in the middle stratum during the wet season. Leaves in the wet season, combined for all strata, had a greater ϵ than those in either of the other seasons, significantly so for the early dry season ($P = 0.02$) and for the combined early and dry seasons ($P = 0.003$).

Discussion

Light Microenvironment

During the dry season, individuals of *Tillandsia brachycaulos* received eight times more daily PPF than the same individuals in the wet season. Such an extreme change in the light environment belies the abundance of *T. brachycaulos* in all strata, covering the stems and canopy of the dry forest trees in the Yucatán

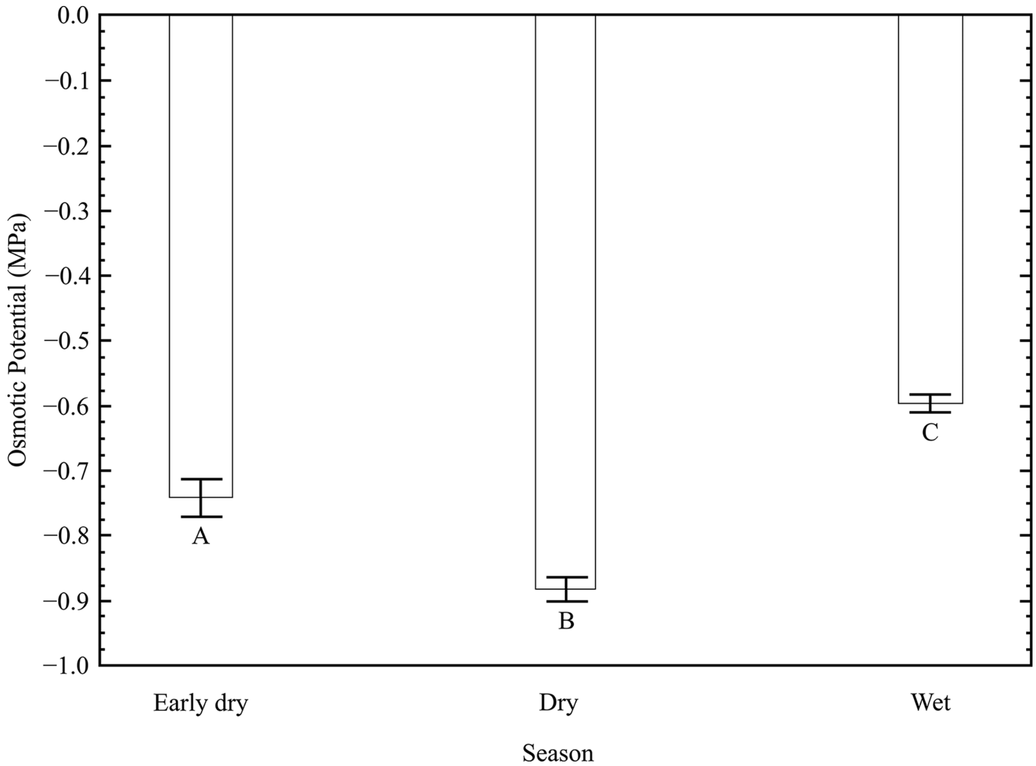

Fig. 4 Osmotic potentials of leaves of *Tillandsia brachycaulos* in the dry deciduous tropical forest of Dzibilchaltún National Park in three seasons. Data are means ± standard errors ($n = 45$). Different letters indicate significant differences (Tukey, $P < 0.05$).

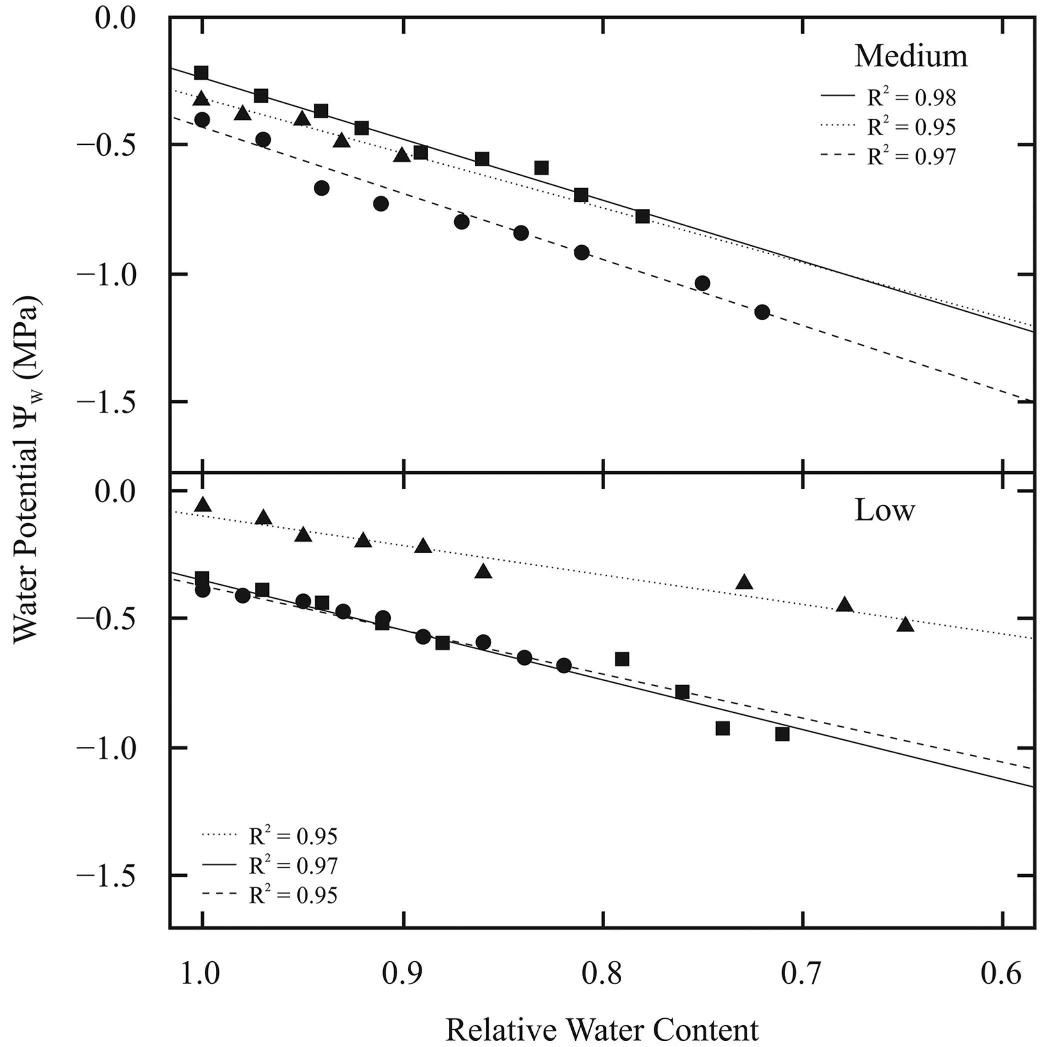

Fig. 5 Water potential isotherms in the early dry season for leaf tissues of *Tillandsia brachycaulos* from plants from the low and medium strata. Different symbols indicate measurements of different individuals.

Peninsula. The ability to acclimate to such a large change in PPF indicates a high photosynthetic plasticity for *T. brachycaulos* and has been observed in several other studies (Graham and Andrade 2004; Cervantes et al. 2005; González-Salvatierra et al. 2010; Cach-Pérez et al. 2018).

Leaf Temperatures

The midday leaf temperatures of *T. brachycaulos* were higher than the air temperature during the early dry and dry seasons, a result of their nocturnal stomatal opening associated with CAM. This increase in the leaf temperature of plants in the lower canopy has been correlated with reduced flowering and growth for *T. brachycaulos* (Cervantes et al. 2005). Midday leaf temperatures were lower than the air temperature for the middle and lower strata during the wet season, most likely due to latent heat loss because of daytime transpiration in well-watered plants of *T. brachycaulos* (Graham and Andrade 2004). Midday leaf temperatures were higher than the air temperature in the wet season for individuals in the upper strata, indicating that water stress during the wet season may still occur for this location in the canopy.

Predawn leaf temperatures that are lower than the air temperature indicate the possibility of dew deposition, a source of water with high water potential (Nobel 2009). This can occur even in the dry season, when most trees are leafless and epiphytes are exposed to a clear, cold sky at night (Andrade 2003; Chávez-Sahagún et al. 2019). Dew and fog events are positively correlated with vascular epiphyte densities and survival during the dry season and are related to epiphyte position in tropical dry forests (Andrade 2003; Graham and Andrade 2004; Reyes-García et al. 2008, 2012; de la Rosa-Manzano et al. 2014*a*; Wu et al. 2018; Chávez-Sahagún et al. 2019).

Plant Water Relations

Leaf osmotic potential was significantly lower in the morning than in the evenings, indicating organic acid production during

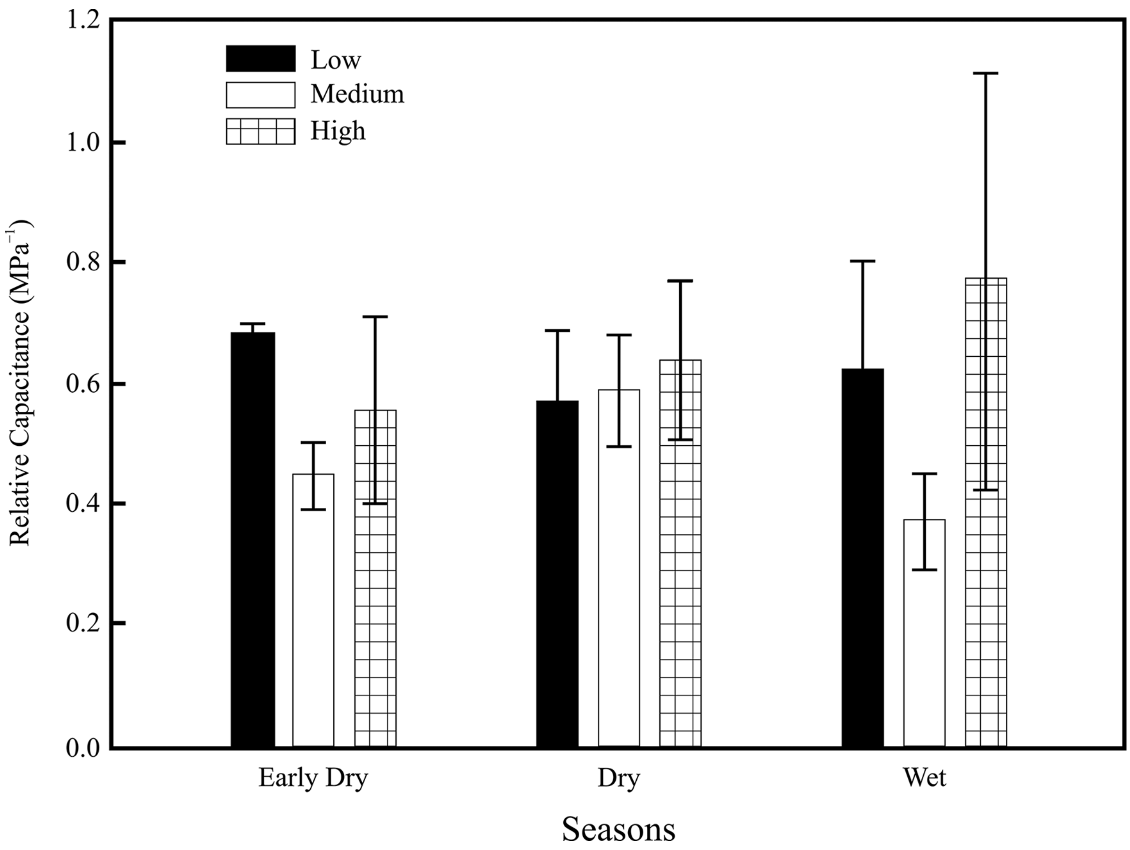

Fig. 6 Relative capacitance of leaves of *Tillandsia brachycaulos* in three different microhabitats and in three seasons in the dry deciduous tropical forest of Dzibilchaltún National Park. Data are means ± standard errors (n = 3).

CAM; the values reported here are similar to those for other epiphytes (Zotz and Hietz 2001; Martin et al. 2004; Cach-Pérez et al. 2018). The relatively low Ψ_π values in the early dry season could be associated with the significantly lower relative capacitance in the middle stratum compared with the low stratum during this time. Indeed, the low relative capacitance of *T. brachycaulos* in the middle stratum could indicate relatively suitable conditions for establishment and growth (Mondragón et al. 2004; Cervantes et al. 2005; Reyes-García et al. 2008; de la Rosa-Manzano et al. 2014*a*), as in other tropical forests (Johansson 1974; Ter Steege and Cornelissen 1989; Nieder et al. 2000).

Osmotic adjustments in epiphytic bromeliads between seasons do not tend to be substantial (Martin et al. 2004), in agreement with our results. A relatively low average leaf ϵ and a high relative capacitance for these plants indicate that water storage capacity may be more important than maintenance of high turgor by means of rigid cell walls and low osmotic potentials (Nowak and Martin 1997). Indeed, when water from rain, dew, or fog is available for these epiphytes, it is at near-zero water potential, and thus low tissue osmotic potentials may not be necessary for water uptake as they might be for plants with roots in a drying soil.

In the combined early dry and dry seasons, *T. brachycaulos* had significantly lower ϵ than during the wet season, indicating that maintenance of turgor by decreasing cell wall elasticity and Ψ_π occurred more under drying conditions. Although we did not examine the water relations among different leaf tissues, other studies have indicated that preferential loss of water from the hydrenchyma is the result of differences in both osmotic potentials and cell wall elasticities (Nowak and Martin 1997).

Table 4

Volumetric Elastic Modulus (ϵ) for Leaves of *Tillandsia brachycaulos* at Three Locations in the Canopy in Three Seasons in the Tropical Dry Deciduous Forest in Dzibilchaltún National Park

Stratum	Early dry (MPa)	Dry (MPa)	Wet (MPa)
Low	1.18 ± .27	2.74 ± .72	2.96 ± 1.45
Middle	2.68 ± .11	2.08 ± .58	5.32 ± 1.01
High	1.43 ± .06	.98 ± .36	3.12 ± .45

Note. Data are means ± standard errors (n = 3).

Conclusions

Our data indicate that the leaf relative capacitance of plants of *Tillandsia brachycaulos* from the middle stratum increased in the dry season but that individuals in all strata maintained high relative capacitance during the year. Osmotic and cell wall elasticity adjustments were modest for this epiphytic species, even though it is exposed to dramatic changes in microenvironment. Such responses are in agreement with the observation that when water is available, it is of high water potential, and thus water storage is the main strategy for surviving in such extreme conditions for this species. Midday high leaf temperatures of *T. brachycaulos* in some microsites indicate low convective heat dissipation without major consequences for its tissue water relations. Further studies with *T. brachycaulos* in common gardens and the laboratory will be necessary for examining its responses to even greater microenvironment variability under climate change conditions.

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