Morphophysiological Plasticity in Epiphytic Bromeliads Across a Precipitation Gradient in the Yucatan Peninsula, Mexico

Authors: Cach-Pérez, Manuel Jesús, Andrade, José Luis, and Reyes-García, Casandra

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Research Article

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Manuel Jesús Cach-Pérez[1,2,3], **José Luis Andrade**[2], and **Casandra Reyes-García**[2]

Abstract

Plasticity may be a key factor to determine plant survival under a changing environment as a result of climate change or land use modification. Plasticity in physiological and morphological traits was evaluated in seven epiphytic *Tillandsia* species (Bromeliaceae) from six vegetation communities along a precipitation gradient in the Yucatan Peninsula, Mexico. Microenvironmental conditions (air temperature and humidity, light, and vapor pressure deficit), as well as Δ titratable acidity, osmotic potential, relative water content, and succulence were characterized during wet, early dry, and dry seasons. We calculated the relative distances plasticity index using physiological data from the wet and dry seasons; morphological plasticity was also calculated for foliar trichome and stomatal traits from previously published data. We found high variation in microenvironmental conditions between seasons, particularly for the tropical dry deciduous forest. The dry season had a negative effect in all physiological variables (decrease from 40% to 59% for Δ titratable acidity and 10% to 38% for relative water content). The highest plasticity was registered for *T. balbisiana* (physiological: 0.29, anatomical: 0.18) and the lowest for *T. fasciculata* and *T. yucatana*. Nonmetric multidimensional scaling analysis separated individuals distributed in the wettest vegetation types from those distributed in the driest vegetation types, irrespective of the species, showing convergent physiological strategies to confront environmental variation. We found higher plasticity in water use traits in atmospheric species, compared to tanks and higher plasticity in general in species with wide distribution compared to those with small distribution ranges.

Keywords

Bromeliaceae, photosynthesis, seasonality, *Tillandsia*, water relations

Introduction

Plasticity can be defined as the ability of an organism to adjust its performance through changes in its morphology or its physiology in response to changes in environmental conditions (Navas & Garnier, 2002; Pigliucci, 2005; Valladares, Sanchez-Gomez, & Zavala, 2006; Valladares, Wright, Lasso, Kitajima, & Pearcy, 2000). This response of individuals (plasticity) to environmental changes influences their distribution and can contribute to plant fitness (Sultan, 2001). The calculation of a plasticity index may be a way to measure the magnitude of these physiological and morphological changes, which can help to understand the strategies followed by plants to cope with environmental variations. It has been proposed that species with wide distribution will show larger phenotypical plasticity than species with restricted distribution, due to their exposition to a wide range of environmental heterogeneity (Chaves, Leal, & Lemos-Filho, 2018; Sultan, 2001; Valladares et al., 2006).

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[1] CONACYT—Departamento de Agricultura Sociedad y Ambiente, El Colegio de la Frontera Sur Unidad Villahermosa, Villahermosa, Tabasco, Mexico
[2] Unidad de Recursos Naturales, Centro de Investigación Científica de Yucatán, A.C., Mérida, Yucatán, Mexico
[3] Laboratorio Nacional de Innovación Ecotecnológica para la Sustentabilidad, Villahermosa, Tabasco, Mexico

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

There is an increasing interest in plant plasticity given the urgency to predict the response of species to climate change (Potvin & Tousignant, 1996; Rehfeldt, Wykoff, & Ying, 2001). This would be important, for example, if we consider that changes on species distribution under climate change are projected using correlations on bioclimatic models that can overestimate species loss, because some key aspects can be ignored, such as plasticity (Hampe, 2004; Thuiller et al., 2005).

The epiphytic habitat can be considered extreme due to high environmental variability. The absence of roots in the soil make epiphytes dependent on atmospheric precipitation (rain, dew, and fog) to acquire water and nutrients and highly sensitive to air humidity in order to maintain water balance (Benzing, 1990; Einzmann & Zotz, 2016). Epiphytes have developed adaptations such as poikilohydry, leaf, stem, and root succulence, and crassulacean acid metabolism (CAM) to cope with variability in water supply (Ng & Hew, 2000; Zotz & Hietz, 2001). In the family Bromeliaceae in addition to CAM photosynthesis and succulent tissues, epiphytic species have foliar trichomes specialized in the absorption of water and nutrients and may also exhibit water reservoirs at the base of its leaves (Benzing, 1990; Chaves, Leal, & de Lemos-Filho, 2015; Freschi et al., 2010; Kleingesinds et al., 2018; Martin, 1994). Regarding these traits, epiphytic bromeliads have been classified in two main life forms: atmospheric species (with lingulate to narrowly triangular leaves, densely covered by trichomes) and tank species (with long and wide leaves that form a water reservoir in the center of the rosette; Benzing, 1980). These morphological differences have been linked to physiological strategies, as tank species maintain a more constant water source that partly isolates them from surrounding environmental conditions, the seasonal variation in water and light use may be more conservative, compared to the atmospheric species (Kleingesinds et al., 2018; Reyes-García, Mejia-Chang, & Griffiths, 2012). These adaptations have allowed bromeliads to colonize habitats in a wide range of environments, from moist montane forests, coastal deserts, and Andean paramos (Benzing, 2000).

Several studies have demonstrated the high sensitivity of epiphytic bromeliads to environmental changes (Andrade, 2003; Chilpa-Galván, Tamayo-Chim, Andrade, & Reyes-García, 2013; De Sousa & Colpo, 2017; Graham & Andrade, 2004; Nowak & Martin, 1997; Reyes-García & Griffiths, 2009; Reyes-García, Griffiths, Rincón, & Huante, 2008; Reyes-García, Mejía-Chang, Jones, & Griffiths, 2008; Valdez-Hernández, González-Salvatierra, Reyes-García, Jackson, & Andrade, 2015; Zotz & Asshoff, 2010). However, these studies have been carried out with particular species, in a few sites or under certain seasons. Only a handful of physiological studies have been performed with epiphytic bromeliad species growing along environmental gradients (Cach-Pérez, Andrade, & Reyes-García, 2014; Griffiths & Maxwell, 1999; Griffiths & Smith, 1983) and none of these have focused in characterizing plasticity, which can help predict possible responses to climate change and possible impacts in the different vegetation types where these species can be found.

The aim of this study was to determine the plasticity of seven epiphytic bromeliads to variation in environmental conditions within six contrasting vegetation types of the Yucatan Peninsula, Mexico, along a precipitation gradient (from 500 to about 1,500 mm y^{-1}). We expected that species with a wider distribution, and located at the drier, more seasonal northwestern region of the Peninsula would show higher plasticity compared with species with limited distribution. We also expected tank species to be less plastic than atmospheric species. We characterized seasonal variations in physiological traits (Δ titratable acidity, leaf relative water content [RWC], leaf osmotic potential, and leaf succulence) under field conditions and used published data on morphological traits to obtain physiological and morphological plasticity indexes.

Methods

Field Sites

Measurements were performed for seven epiphytic bromeliad species from six contrasting vegetation types, which follow a precipitation gradient in the Yucatan Peninsula (Mexico; Figure 1): coastal sand dune scrub (21°19 N, 89°26 W; 500 mm mean annual precipitation), scrub and peten mangrove (20°51 N, 90°22 W; 675 mm mean annual precipitation), deciduous forest (21°05 N, 89°35 W; 900 mm mean annual precipitation), semideciduous forest (20°05 N, 89°32 W; 1,150 mm mean annual precipitation), and semievergreen forest (18°06 N, 89°48 W; 1,500 mm mean annual precipitation); the sites are described in detail in Cach-Pérez et al. (2013).

Studied Species

For the physiological measurements, we selected seven species of the 15 reported by Cach-Pérez et al. (2013) according to their distribution, abundance, and importance value index within each vegetation type. At each site, we surveyed a tank and an atmospheric species, in order to contrast the strategies, except for the peten mangrove where *Tillandsia streptophylla* Scheidw. was the only abundant species. The selected species were *Tillandsia brachycaulos* Schltdl., *Tillandsia dasyliriifolia* Baker, *Tillandsia balbisiana* Schult.f., *Tillandsia elongata* var. *subimbrincata* (Baker) L.B.Sm, *Tillandsia fasciculata*

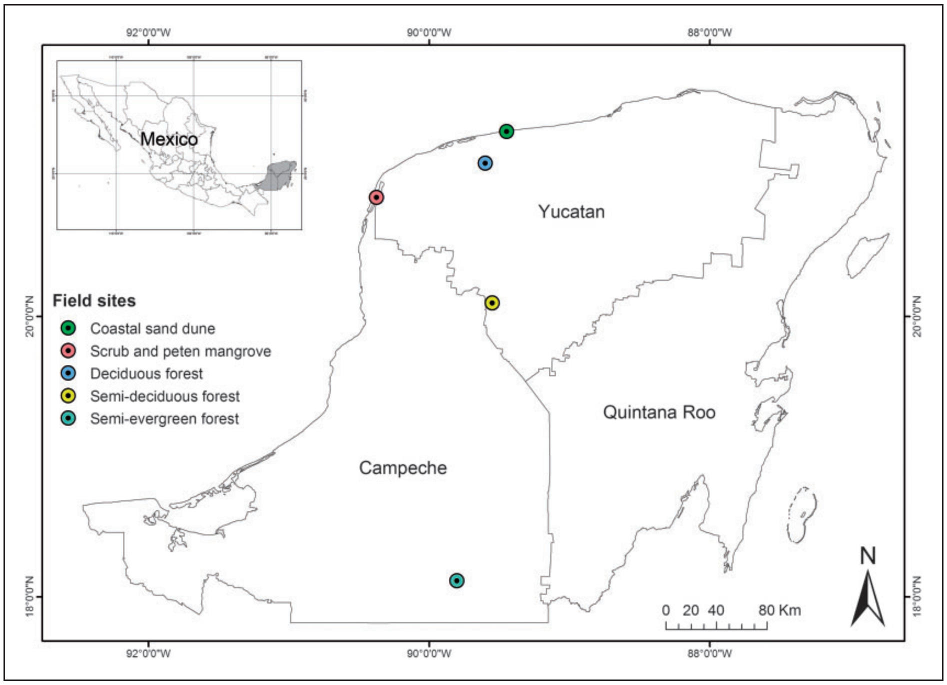

Figure 1. Map of the five field sites where epiphytic bromeliads were sampled in the Yucatan Peninsula, Mexico.

Table 1. Study species life form and distribution.

Species/vegetation type	Life form	Coastal scrub	Scrub mangrove	Peten mangrove	D forest	SD forest	SE forest
Tillandsia balbisiana Schult.f.	A	P,M			*	M	*
Tillandsia brachycaulos Schltdl.	A				P,M	P	P,M
Tillandsia dasyliriifolia Baker	T	P,M	P		*		M
Tillandsia elongata var. *subimbricata* (Baker) L.B.Sm	T				P	*	*
Tillandsia fasciculata Sw.	T				*	P	P
Tillandsia streptophylla Scheidw.	A			P			
Tillandsia yucatana Baker	A	M	P		M		

Note. The letters denote life forms (A = atmospheric; T = tank), and the sites where the species were collected for physiological (P) or morphological (M) measurements. Asterisks denote the presence of the species at the site. Sites are abbreviated as coastal scrub = coastal sand dune scrub; Forests: D = deciduous; SD = semideciduous; and SE = semievergreen.

Sw., *T. streptophylla*, and *Tillandsia yucatana* Baker. The vegetation type where each species is found and the species life form are shown in Table 1.

Microenvironment

We measured photon flux density (PFD), temperature, and humidity of the air at a mid-canopy height on each vegetation type, where most of the epiphytic bromeliads are located (Cach-Pérez et al., 2013). We used quantum sensors (S-LIA-M003), temperature, and relative humidity sensors (S-THB-002), connected to a data logger (HOBO micro station H21-002). All the sensors and data loggers were from Onset (Bourne, MA). Measurements were made during the wet, early dry, and dry seasons for at least 4 days per season, between July 2009 and May 2011. A second microenvironment station was simultaneously installed in an open site as a reference. Vapor pressure deficit (VPD) was calculated using air temperature and relative humidity following Jones (1992).

Physiological Measurements

Titratable acidity. We collected leaf samples at sunset and predawn of the following day. Samples were frozen in liquid nitrogen for 24 hr, and sample area was determined with a leaf area meter (Li-3100, LI-COR, Lincoln, NE).

Samples were then macerated in a porcelain mortar, added to 60 ml of distilled water, and boiled for 6 min. After cooling to ambient temperature, samples were titrated with sodium hydroxide (NaOH) 0.01 N with an automatic titrator (702 SM Tritino, Metrohm, Switzerland). Titratable acidity (mmol H^+ m^{-2}) is reported as delta value (ΔH^+) calculated as titratable acidity at dawn minus titratable acidity at sunset. On each case, titratable acidity was calculated as

$$\Delta H^+ = \frac{\text{NaOH consumed} \times \text{NaOH normality}}{\text{Leaf area}} \times 100$$

Osmotic potential. Fragments of the leaf samples collected for ΔH^+ at pre-dawn were also used to determine the osmotic potential. Frozen samples were macerated in a porcelain mortar to obtain expressed sap that was used to wet a filter paper disc of 0.38 cm^{-2}. The disc was placed in an osmometer (VAPRO 5520, Wescor, Logan, UT) to obtain the sample osmolality from which osmotic potential (MPa) was calculated as

$$\text{Osmotic potential} = \left(2.479 \times 10^{-3}\right)(\text{Osmolality})(-1)$$

RWC and succulence. Leaf samples were collected, weighted (fresh weight), placed to saturate in distilled water for 48 hr, and weighted again (saturated weight). Later, samples were dried at 65°C for 48 hr and weighted (dry weight). Sample area was determined after fresh weight with a leaf area meter (Li-3100, LI-COR, Lincoln, NE). RWC and leaf succulence was calculated after González and González-Vilar (2003) as

$$\text{RWC} = \frac{\text{Fresh weight} - \text{Dry weight}}{\text{Saturated weight} - \text{Dry weight}} \times 100$$

$$\text{Succulence} = \frac{(\text{Fresh weight} \ - \text{Dry weight})\ (1,000)}{\text{Leaf area}}$$

All leaf samples used in physiological measurements were collected from the middle part of the rosette from five individuals per species, per vegetation type, during the wet, early dry, and dry seasons between July 2009 and September 2011. All the samples were taken from the same individual during the study.

Plasticity Index

To integrate physiological and microenvironmental data associated to the response of epiphytic bromeliads to environmental variation, we calculated the plasticity of the physiological variables measured, for each species in the vegetation types. We used the plasticity index based on phenotypic relative distances (RDPI) following Valladares et al. (2006), Scoffoni et al. (2015), and de la Rosa-Manzano, Andrade, Zotz, and Reyes-García (2017) as

$$\text{RDPI} = \sum\left(d_{ij} \rightarrow i'j'/\left(x_{i'j'} + x_{ij}\right)\right)/n$$

where $d_{ij} \rightarrow i'j'/\left(x_{i'j'} + x_{ij}\right)$ is the relative distance defined for all pairs of individual samples taken of the different vegetation types, and n is the number of replicates. The index was calculated for physiological data obtained in the two most contrasting seasons (wet and dry); subsequently, we calculated the mean phenotypic plasticity for each species per site considering the mean RDPI value obtained for each variable measured. The index varies from zero (*no plasticity*) to one (*high plasticity*). For species distributed on more than one vegetation type, we used data from Cach-Pérez, Andrade, Cetzal-Ix, and Reyes-García (2016) on morphological variables to calculate the morphological plasticity. The variables used were trichome density, trichome shield area, total trichome area, stomatal density, stomatal pore size, and total stomatal size. The index was calculated using data from the two most contrasting vegetation types within each species range.

Statistical Analyses

We used a one-way analysis of variance to compare variations on microclimatic conditions between seasons. A repeated measures analysis of variance was used to identify differences in physiological traits between seasons and vegetation types (on epiphytic bromeliads distributed in more than one vegetation type). Data were checked for normality and homoscedasticity prior to the analyses. Significance level was $\alpha = 0.05$, and Tukey post hoc tests were applied in all cases. Statistica 8.0 software (StatSoft, Inc. 1984–2007, Tulsa, OK) was used for all tests.

A nonmetric multidimensional scaling (NMDS) analysis using physiological data of each species per study site was performed using vegan package for R version 3.4.0 (Oksanen et al., 2017; R Core Team, 2017) to identify similarities on the physiological strategies used by each species under different environmental conditions inherent to each vegetation type.

Results

All vegetation types presented variation in PFD and VPD between seasons ($p < .05$). The most extreme microenvironmental conditions were registered for the dry deciduous forest with a contrasting variation in PFD and VPD conditions between seasons (PFD was 60% higher during the dry season than during the wet season). However, the highest seasonal variation in VPD occurred for the semideciduous and the semievergreen forests with an increase of 85% and 86% during the dry season compared to the wet season (Figure 2). The vegetation types with less microenvironmental variation along the characterized seasons were the peten mangrove and the semievergreen forest (Figure 2). The highest values of PFD and VPD were registered during the dry season for all vegetation types, except for the scrub mangrove that presented similar values of VPD between seasons.

Regarding physiological plasticity, the highest physiological plasticity index (RDPI c. 0.3) was registered for *T. balbisiana* followed by *T. streptophylla, T. elongata*, and *T. brachycaulos* (Figure 3). The morphological plasticity index for epiphytic bromeliad species distributed in more than one vegetation type was generally lower than the physiological plasticity index, except in the case of *T. dasyliriifolia* (Figure 3). *T. dasyliriifolia* presented the highest morphological plasticity, whereas *T. fasciculata* showed the lowest plasticity.

Individual physiological and morphological variables showed an uneven contribution to the global species plasticity. High physiological plasticity was observed in ΔH^+ for all species, followed by succulence (Figure 4). On the other hand, osmotic potential and relative water content were less plastic, especially in species distributed in the coastal sand dune scrub, scrub mangrove, and peten mangrove. The most plastic morphological traits were stomatal and trichome size (Figure 5).

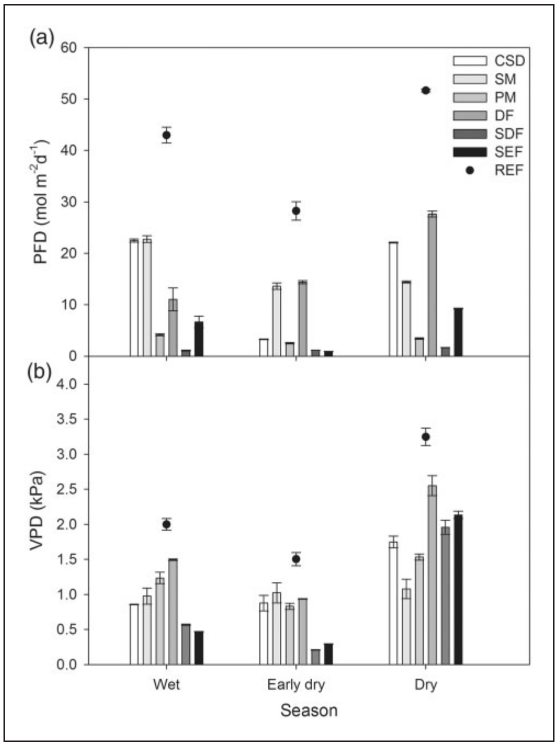

Figure 2. Photon flux density (a) and vapor pressure deficit (b) registered on six vegetation types of the Yucatan Peninsula during wet, early dry, and dry seasons.
CSD = coastal sand dune scrub; SM = scrub mangrove; PM = peten mangrove; DF = dry deciduous forest; SDF = semideciduous forest; SEF = semievergreen forest; REF = reference; VPD = vapor pressure deficit; PFD = photon flux density. Data are means ± standard error.

The NMDS analysis (Figure 6) arranged the individuals from the scrub and peten mangroves, and some from the dry deciduous forest, in the more negative values of the first axis, and the rest of the individuals of the forests and coastal sand dune scrub near zero or with positive values, irrespective of the species. *T. yucatana* appeared to have a physiological strategy that was very different from the other species (high succulence and ΔH^+ along the year, see Supplementary Material), and which was opposed to the strategy of *T. brachycaulos* from the semievergreen forest (low ΔH^+ and high variation in osmotic potential along the year, Supplementary Material; Figure 6). The species *T. dasyliriifolia* had similar physiological strategies in the two sites where individuals can be found (low variation on physiological parameters). Individuals of *T. brachycaulos* showed similar physiological strategies in vegetation types with similar microclimate (the semideciduous and semievergreen forests) but showed divergent traits in individuals distributed in the drier deciduous forest. The analysis showed that carbon assimilation (measured as ΔH^+) was the main factor that drives species ordination (Table 2), specifically species response during the early dry season. Water status along the year (mainly succulence) was also important to define the physiological response for epiphytic bromeliads growing on contrasting vegetation types, according to the NMDS analysis.

Discussion

In accordance to our initial hypothesis, *T. balbisiana*, the species with the widest distribution (found in the coastal sand dune scrub and all three forests, Table 1) had the highest overall physiological plasticity and the second highest morphological plasticity (RDPI, Figure 3). Although this species was only surveyed physiologically at one site (because it generally had small populations), it showed high plasticity in response to seasonal environmental changes. This is consistent with that found in two tank bromeliad species from a wet forest, where the species with the wider range also showed the highest plasticity (North et al., 2016). The relationship between distribution range and plasticity was not as clear in the rest of the species in our study. We expected the species from the more seasonal northwestern region of the Peninsula to show high plasticity, and this was observed in *T. streptophylla*, a species limited to the peten mangrove, but not in *T. yucatana*, also limited to the northwest and with the lowest plasticity of all the species. There were also differences in plasticity among

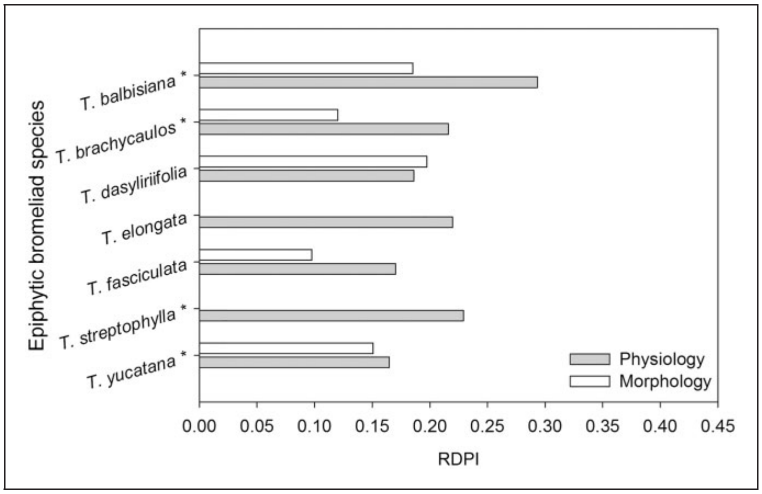

Figure 3. Physiological plasticity index for seven epiphytic bromeliads distributed on six vegetation types (dark gray bars) and morphological plasticity index for epiphytic bromeliad species distributed on more than one vegetation type (grey bars). RDPI = relative distance plasticity index. Asterisks indicate atmospheric species.

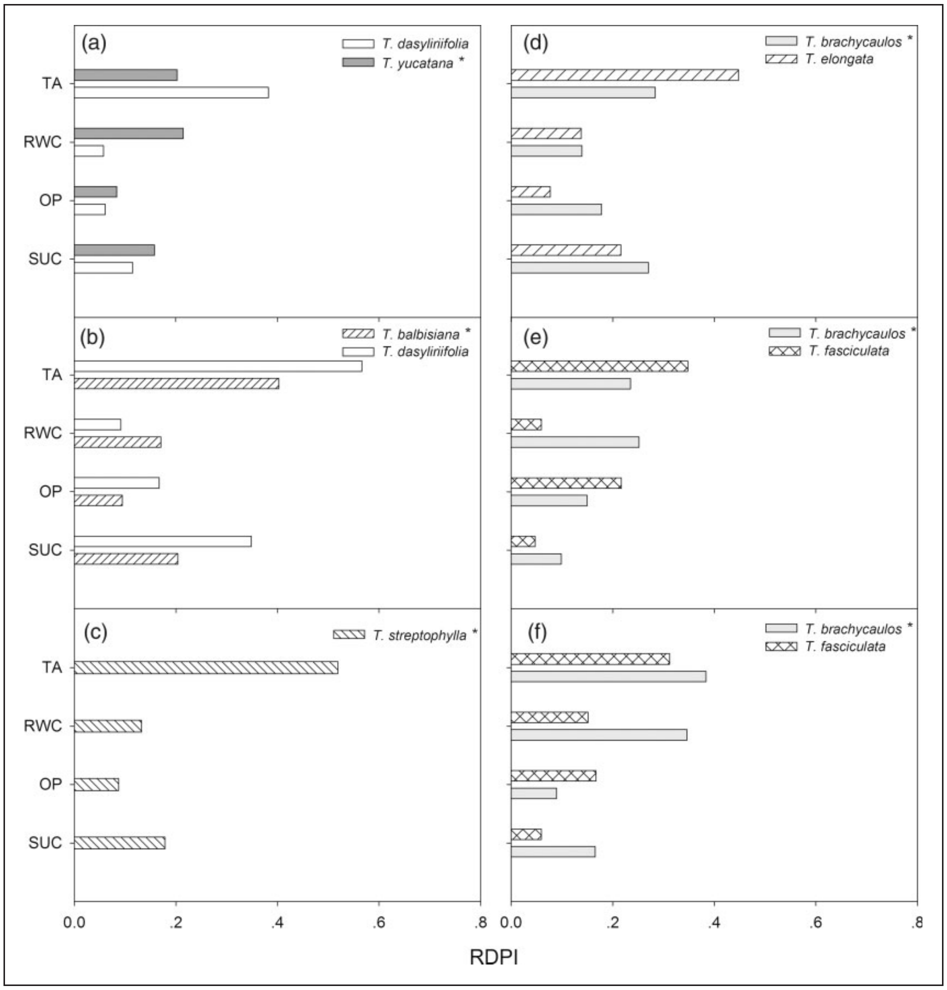

Figure 4. Plasticity index calculated for each physiological trait measured per species, distributed on each vegetation type. (a) Scrub mangrove; (b) coastal sand dune scrub; (c) peten mangrove; (d) dry deciduous forest; (e) semideciduous forest; and (f) sub-perennial forest. TA = delta tritatable acidity; RWC = relative water content; OP = osmotic potential; SUC = succulence. Asterisks indicate atmospheric species; RDPI = relative distance plasticity index.

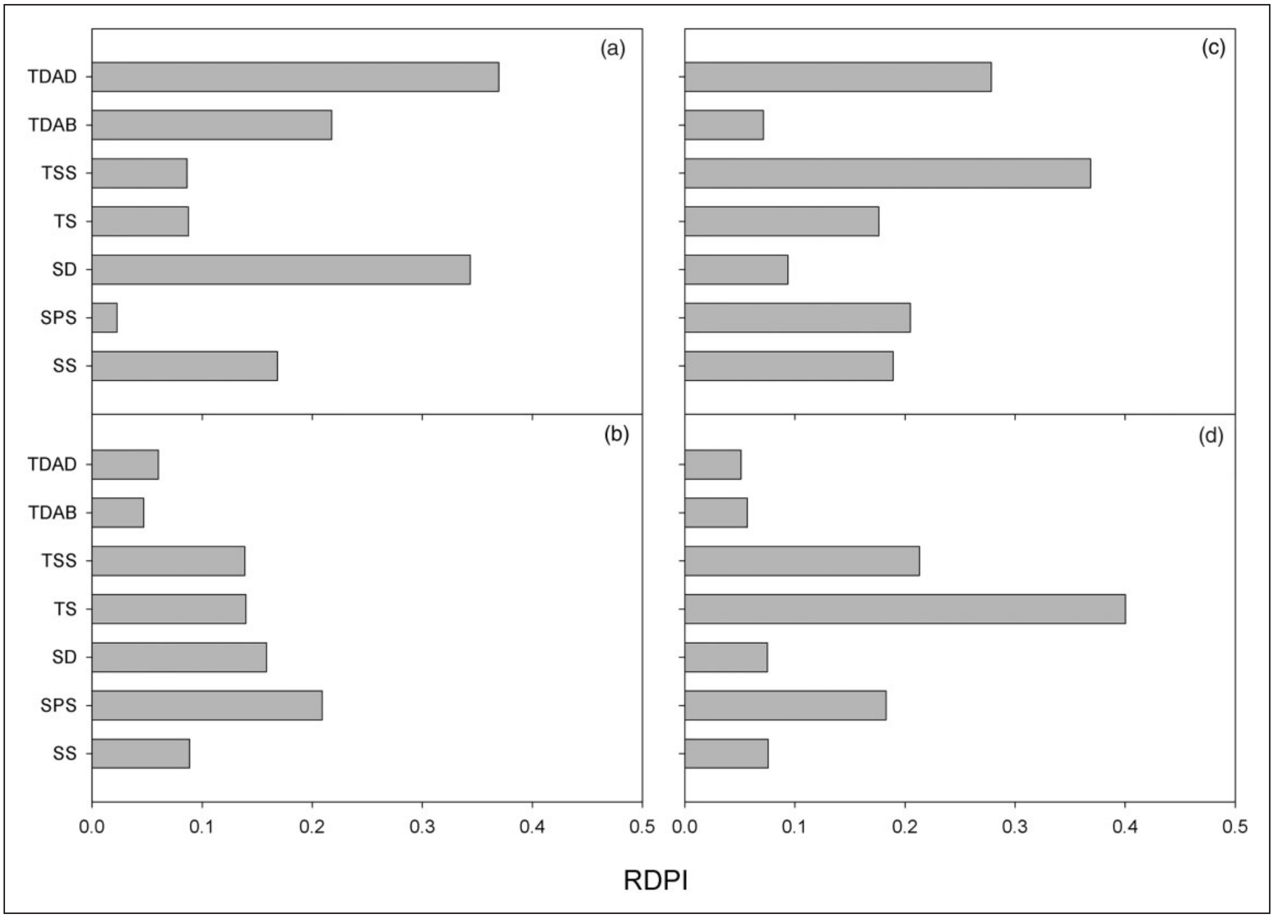

Figure 5. Plasticity index calculated from morphological variables published by Cach-Pérez et al. (2016) for four epiphytic bromeliad species distributed on more than one vegetation type. (a) *T. balbisiana**; (b) *T. brachycaulos**; (c) *T. dasyliriifolia*; (d) *T. yucatana**. TDAD = trichome density on adaxial leaf face; TDAB = trichome density on abaxial leaf face; TSS = trichome shield size; TS = trichome size; SD = stomatal density; SPS = stomatal pore size; SS = stomatal size; RDPI = relative distance plasticity index. Asterisks indicate atmospheric species.

T. brachycaulos, *T. elongata*, and *T. fasciculata*, all of which coexisted in the three surveyed forests but were not found in the other environments.

Atmospheric species were not shown to have higher overall plasticity compared to tank species (Figure 3), as our second hypothesis stated. Nevertheless, when we analyzed the plasticity in the different physiological traits, within each environment for which we had paired measurements of tank and atmospheric species, the atmospheric species had higher plasticity regarding RWC and succulence, both traits related to water use (Figure 4). In contrast, the tank species showed higher plasticity in Δ titratable acidity (ΔH^{+}). These physiological differences are also evident in the NMDS analysis, which showed a segregation of tank and atmospheric species according to the second axis. This same pattern (high plasticity in acidity and low in RWC) was found in Chaves, Leal, and de Lemos-Filho (2018) for three tank species. Tank species may have higher carbon assimilation when water in the tank provides a stable water source but then suppress carbon gain through stomata closure to maintain stable RWC values when the tank is dry (Adams & Martin, 1986; Graham & Andrade, 2004; Reyes-García, Griffiths, et al., 2008). On the other hand, the two tank species *T. fasciculata* and *T. dasyliriifolia* had higher plasticity in osmotic potential than the rest of the species. Low osmotic potential has been related to osmotic adjustment in the later species (Cach-Pérez, 2013). In general, the RDPI values reported here were similar or higher than those reported in other CAM epiphytes (Bromeliaceae, Chaves et al., 2018; Orchidaceae, de la Rosa-Manzano et al., 2017) but lower than those reported for C_3 epiphytes (with the exception of *T. balbisiana*; Pires, de Almeida, Abreu, & da Costa Silva, 2012).

Plastic or nonplastic water use traits appear to be among the most important factors driving horizontal distribution of species (Cach-Pérez et al., 2013; Males, 2016;

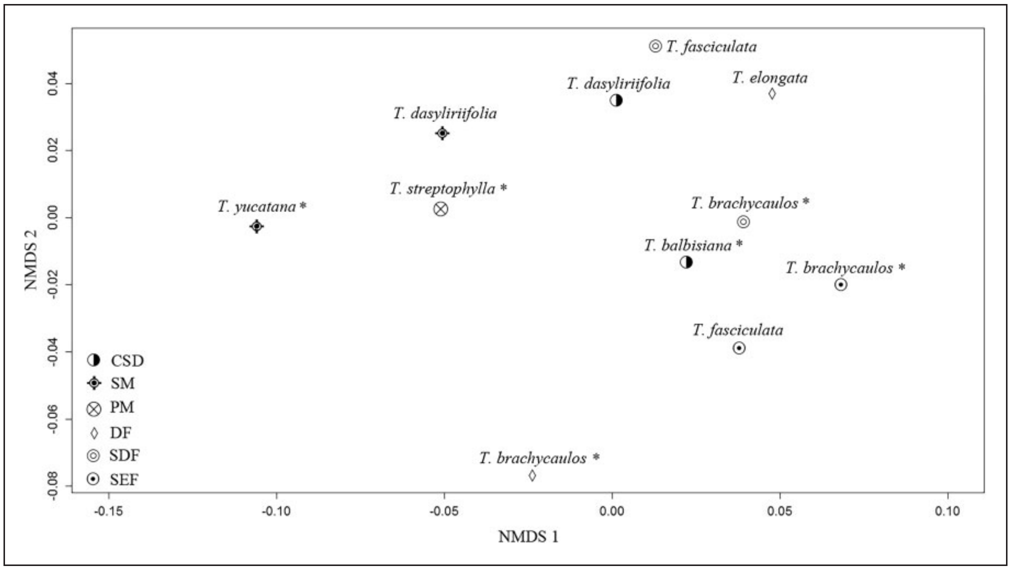

Figure 6. NMDS analysis for physiological traits of seven epiphytic bromeliad species (stress = 0.11).
CSD = coastal sand dune scrub; SM = scrub mangrove; PM = peten mangrove; DF = dry deciduous forest; SDF = semideciduous forest; SEF = semievergreen forest; NMDS = nonmetric multidimensional scaling. Asterisks indicate atmospheric species.

Table 2. Principal Physiological Trait Scores to Species Ordination on NMDS Analysis (Stress = 0.11).

Physiological trait (season)	NMSD1	NMSD2
Delta titratable acidity (early dry)	−0.0809	0.0023
Succulence (dry)	−0.0624	0.0058
Relative water content (wet)	0.0612	−0.0045
Succulence (early dry)	−0.0587	−0.0141
Succulence (wet)	−0.0541	−0.0169
Osmotic potential (dry)	0.0481	−0.0283
Relative water content (early dry)	0.0433	−0.0037

Note. NMDS = nonmetric multidimensional scaling.

Ramírez, Carnevali, & Chi, 2004). There was less variation within the different physiological parameters measured in plants distributed in wetter sites than drier ones, even though the wetter semievergreen forest also experienced dramatic seasonal changes in VPD. The adverse conditions in the driest vegetation types, mainly at the coastal sand dune scrub (as the scrub mangrove maintained low VPD all year round, diminishing the effect of the dry period), was correlated to the development of different morphological modifications; for example, trichome density and size were higher in atmospheric bromeliad species distributed in drier sites than in wetter sites of the Yucatan Peninsula, probably playing a photoprotective role and aiding against desiccation by shielding the stomata (Cach-Pérez et al., 2016; Pierce, 2007).

Although the NMDS analysis grouped together different species, located at similar environments (Figure 6), contrasting strategies at the species level can also be observed. For example, *T. brachycaulos* from the semideciduous and semievergreen forest grouped close together with *T. fasciculata* from the latter forest. In contrast, *T. brachycaulos* from the deciduous forest was segregated from this group, highlighting different values in physiological parameters. Contrasting strategies at a species level were also observed; at one extreme, *T. yucatana* from the scrub mangrove maintains high succulence and high ΔH^+ year round, while at the other extreme, *T. brachycaulos* from the semievergreen forest has low succulence, low ΔH^+ and high seasonal fluctuations in osmotic potential (Supplementary Material). *T. yucatana* showed surprisingly stable physiological values along year, despite being located in environments with the highest seasonality in rain. The stability may be aided by the high succulence that increases water reserves, and the night-time gas exchange under the humidity-saturated environment near the coast (Figure 2) which can mean high carbon exchange coupled to near zero net water loss (Reyes-García, Mejia-Chang, et al., 2008). The sustained high radiation under this more exposed environment allows for high carbon assimilation year-round.

Implications for Conservation

Epiphytes are among the groups most threatened by climate change due to their sensitivity to environmental variation (Cach-Pérez et al., 2014; Wagner & Zotz, 2016). In this regard, plasticity is expected to favor survival under climate change. Nevertheless, our results highlight that species highly equipped to deal with environmental stress may also show very low plasticity. This was the case of *T. yucatana*, which exhibits high succulence that is coupled to high resistance to drought, resistance to high temperatures and high light, and has the lowest plasticity value of the studied species. Under the scenario of increased temperatures and decreased precipitation, *T. yucatana* would be expected to be successful, regardless of the low plasticity. In addition, other traits such as tank water holding capacity and plant size would need to be studied to have a more complete assessment of the species' strategy. Greenhouse studies may also be relevant to discern the specific effect that changes in temperature, rain, and light may have in individual species survival, and the role that its physiological and morphological plasticity plays in this.

On the other hand, epiphytic bromeliads have also been proposed as potential early indicators of ecosystem stress from climate change (Cach-Pérez et al., 2014). Based on our results, we would expect those species with lower plasticity to serve better as markers (through either a decrease or an increase in population numbers), compared to the more plastic species which have a higher chance of acclimating to the new conditions.

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