

Biomass, phorophyte specificity and distribution of *Tillandsia recurvata* in a tropical semi-desert environment (Chihuahuan Desert, Mexico)

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Background and aims – In low-precipitation environments, vascular epiphytes are expected to present low abundance and species richness, and could be restricted to inhabit a small number of phorophyte species. At the northern limit of the tropical region, in the southern Chihuahuan Desert, we determined epiphyte richness and biomass, and we tested whether *Tillandsia recurvata* exhibits phorophyte preference and whether vertical preference was exhibited within *Prosopis laevigata*.

Material and methods – In thirteen study sites covering the San Luis Potosi high plateau, southern area of the Chihuahuan Desert, Mexico, we established five parallel transects (10 × 50 m). In those transects, we sampled the epiphyte richness and we recorded the frequency of *Tillandsia recurvata* on its phorophyte species, and the abundance and the vertical distribution of *T. recurvata* on *Prosopis laevigata*.

Key results – As expected, richness of holoeipiphytes was weak (only one species: *T. recurvata*). Frequency of *T. recurvata* between the phorophyte individuals was high (41% to 100% of the individuals) considering all phorophyte species. Dry biomass of *T. recurvata* ranged from 0 to 9.4 kg per tree, and in the scrubland, ranged from 8.3 ± 18.4 kg/ha to 491.9 ± 92.3 kg/ha. Vertical distribution of the dry biomass of *T. recurvata* on *P. laevigata* was similar between outer (15.1 ± 15.7 gr/m of bark) and inner branches (12.2 ± 13.6 gr/m of bark), but was lower on the trunk (0.8 ± 1.4 g/m² of bark).

Conclusions – Our study shows that in our study area, one epiphyte species is present but it can invade all phorophyte species, most of the available phorophyte individuals and most of the vertical habitats. Even when precipitation limits the epiphyte richness, a single holoeipiphyte species can reach biomass similar to that found in humid montane forest.

Key words – Bromeliaceae, epiphyte dry biomass, host preference, vertical stratification.

INTRODUCTION

Biogeographical evidence shows that epiphyte species richness and abundance decreases along with precipitation (Gentry & Dodson 1987, Wolf & Flamenco 2003). One possible explanation for this phenomenon is that the lack of a constant water supply restricts the development of certain epiphytic species (e.g. Hymenophyllaceae) in most arid environments.

Despite a broad understanding regarding which climatic factors maintain low epiphyte richness in environments with low precipitation, there is no agreement regarding which ecological elements explain epiphyte abundance in these environments. In dry environments epiphytes usually do not create a suspended soil on the branches of their phoro-

phytes, making the direct interaction with phorophytes more important in determining epiphyte abundance (Hofstede et al. 2001). In some semi-desert scrublands and tropical dry forests, epiphytes present low abundance and are restricted to few phorophyte species (García-Suárez et al. 2003, Bernal et al. 2005, Vergara-Torres et al. 2010). Hypotheses such as phorophyte preference and phorophyte limitation have been proposed as explanations for these patterns (Bernal et al. 2005, Valencia-Díaz et al. 2010, Vergara-Torres et al. 2010). However, it has been suggested that epiphytes could potentially inhabit all phorophyte species within a forest, because trees must be facilitators for epiphytes (Callaway et al. 2002, Vergara-Torres et al. 2010). Additionally it is common to found epiphyte species on artificial phorophytes, such

as power lines, reinforcing the expectation that epiphytes should be able to colonize any substrate (Wester & Zotz 2010).

At the northern limit of the tropical region, in the southern Chihuahuan Desert, epiphytic bromeliads such as *Tillandsia recurvata* (L.) L. and *T. usneoides* L. have been described as being visually highly abundant (Rzedowski 1978, Benzing 1990) but no study has recorded epiphyte abundance numerically in this semi-desert. In another woodland area, the high abundance and frequency of epiphytes has made forest managers to consider epiphytes, like *T. recurvata*, to be weeds and they are thought to be harmful to trees (Caldiz & Fernandez 1995).

The main objectives of this study were: a. to estimate the biomass of *Tillandsia recurvata* in the southern Chihuahuan Desert, and b. to test if *T. recurvata* can develop a wide distribution among phorophyte species and inside the strata of the most abundant host. In order to do so, we determined the frequency of *T. recurvata* on phorophyte species and the abundance and vertical distribution of *T. recurvata* on *Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C. Johnst. We hypothesized that a. if visual reports regarding the abundance *T. recurvata* are accurate, the biomass of *T. recurvata* will be high, and b. if *T. recurvata* reaches a high frequency among phorophyte species, this supports the theoretical expectation

that epiphytes can be highly frequent among phorophyte species (Callaway et al. 2002). However, if *T. recurvata* populations are restricted to certain phorophyte species only, this will provide evidence to support the empirical studies that show that epiphytes cannot invade all available phorophyte species abundantly, because of mechanisms such as phorophyte preference and phorophyte limitation.

MATERIALS AND METHODS

Study area

The study was conducted in the scrublands of the southern Chihuahuan Desert in Mexico, at the northern limit of the tropical region on the high plateau of San Luis Potosí (fig. 1, table 1). In the studied scrubland, altitude ranges between 1000 and 2300 m a.s.l. (INEGI 2003). Mean annual precipitation at this location ranges from 300 to 500 mm and mean annual temperature is between 13°C and 18°C. The shrub vegetation of the area is mainly composed of *Larrea tridentata* (Sessé & Moc. ex DC.) Coville (Zygophyllaceae), *Flourensia cernua* DC. (Asteraceae), *Opuntia* spp. (Cactaceae), *Yucca* spp. (Asparagaceae), *Acacia* spp. and *Prosopis laevigata* (Fabaceae), and is dominated in some areas by *Agave* spp. (Asparagaceae), *Hechtia glomerata* Zucc. (Bromeliaceae) and *Dasylium* sp. (Liliaceae) (Rzedowski 1978).

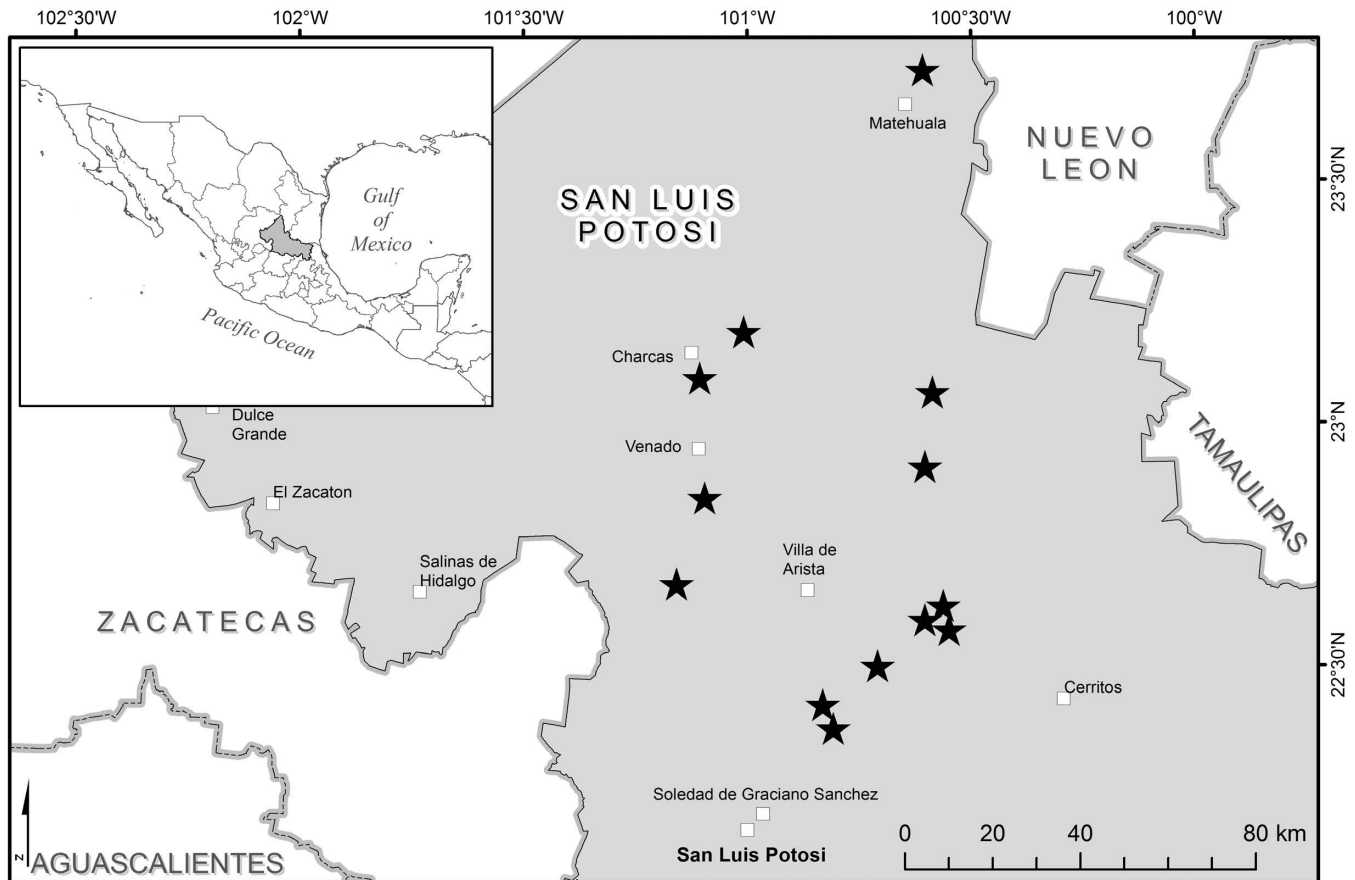


Figure 1 – The thirteen study site locations (solid stars) in the scrublands of the southern Chihuahuan Desert on the San Luis Potosí high plateau, Mexico. Empty squares are the main towns in the area.

Table 1 – The thirteen study site locations in the scrublands of the Chihuahuan Desert on the San Luis Potosi high plateau, Mexico.

For each location, the UTM coordinates and altitude are shown. Location names correspond to the nearest town within the study area.

Name	UTM X	UTM Y	Altitude (m a.s.l.)
Cerrito	340873	2501771	1496
Chorrillo	342335	2496365	1493
Coyote	336829	2533595	1400
Goleta	313372	2479216	1839
Hormiga	285522	2553622	1926
Jagüey	325821	2488167	1651
Mamiroso	286496	2526272	1779
Pecari	315778	2473850	1835
Pedernal	280172	2506841	1861
Perritos	336243	2623984	1569
Pocitos	295426	2564255	1978
Río Verde	336833	2498684	1507
San Francisco	338577	2550465	1347

Field sampling

Using digital maps (INEGI, Landsat and Google earth), we selected thirteen study sites covering the San Luis Potosi high plateau (fig. 1, table 1). We selected sites where the scrubland was physiognomically dominated by tall shrubs (> 3 m in height) and avoided areas exclusively covered by *Larrea tridentata*, in which large shrubs were infrequent. In each study site, we established five parallel transects (10 × 50 m), some 50 m apart (total number of transects is 65). In each transect, we marked all *Prosopis laevigata* individuals (using Fiber Enviro-Flagging™ tape). For each individual *P. laevigata*, we measured height (Crain fiberglass telescoping measuring rod, 11 m ± 0.5 cm precision), diameter at the base of each trunk (Forestry Suppliers metric fabric diameter Tape, 160 cm ± 0.1 cm precision), two diameters of the crown (the maximum and its perpendicular axis; commercial measuring tape 30 m, ± 0.1 cm precision) and devised an index of *Tillandsia recurvata* cover by visually dividing each tree into three vertical strata (trunk, inner branches and outer branches). To distinguish between inner and outer branches, the crown was visually divided in two equal sections, with the outermost section comprising all of the outer branches. For each stratum, we determined five categories of *T. recurvata* cover: (0), where the stratum was free of *T. recurvata*; (1) if *T. recurvata* cover was between 1% and 25%; (2) for *T. recurvata* cover of between 26% and 50%; (3) for cover between 51% and 75%; and (4) for cover > 75%. The *T. recurvata* cover index of each tree was the sum of the values recorded for each stratum and could range from a minimum of 0 (free of *T. recurvata*) to a maximum of 12 (all strata with *T. recurvata* cover > 75%). We also counted and identified the number of other epiphytic plants that were growing on the *P. laevigata* under survey.

Phorophyte preference

We recorded the presence of *Tillandsia recurvata* in every plant greater than 1.7 m in height (thirteen species, table 2), in two transects randomly selected from the thirteen study sites. Since some phorophyte species were low in abundance, we added individuals that were adjacent to the transect to these observations.

Biomass and vertical distribution of *Tillandsia recurvata* in *Prosopis laevigata*

In order to determine the biomass and vertical distribution of *Tillandsia recurvata* on *Prosopis laevigata*, we collected *T. recurvata* individuals from a sample of the surveyed *P. laevigata* trees. All the *P. laevigata* trees surveyed were categorized according to their height and *T. recurvata* cover index determined (table 3). For collection of *T. recurvata*, we randomly selected at least one tree from each category, with three exceptions (table 3), and from those trees with *T. recurvata* cover index equal to 0.

In each selected tree, we collected all *T. recurvata* individuals growing on the trunk; however, as the tree structures became more abundant in branches, we chose 10–30% branches randomly from each vertical stratum (inner branches and outer branches). Bark area (available surface for epiphyte establishment) was measured for each stratum and estimated for the whole tree. In order to determine bark area where epiphytes were collected, we measured the length and two circumferences (beginning and end) of each tree structure, and used the formula of truncated cone to calculate the bark area for each section. Tree structure was taken to be a single branch or trunk section until its first bifurcation, following van Pelt et al. (2004). Collected *T. recurvata* was dried to 70°C until reaching a constant weight.

Data analysis

Phorophyte preference – We tested whether the proportion of individuals that hosted *Tillandsia recurvata* differed between nine phorophyte species. For this analysis, we used phorophyte species with at least twenty individuals within the entire sample and excluded those that always hosted *T. recurvata* (four species), since variance is zero in these species. We used a χ^2 analysis for testing differences among more than two proportions (Zar 2010). As the test revealed significant differences between phorophyte species, we performed a Tukey-type multiple comparisons test among proportions (Zar 2010) to determine which phorophytes differed significantly.

Abundance of *Tillandsia recurvata* in *Prosopis laevigata* – Biomass of *T. recurvata*, and/or bark area of the sampled *P. laevigata*, was calculated following a three-step analysis method. The first step consisted of calculating the biomass/bark area in each sampled tree. For this purpose, we summed the biomass/bark area of each vertical stratum. In order to estimate the biomass/bark area in vertical strata in which these variables were not completely measured, we multiplied the average of the values of the sampled branches by the total number of branches in the stratum of each tree, as is done in

Table 2 – Density and percentage of individuals of the shrub community (height > 1.7 m), that host *Tillandsia recurvata*.

Data sourced from two transects randomly selected in each of thirteen study sites in the Mexican Chihuahuan Desert. Different letters indicate significant differences in the percentage of frequency of *T. recurvata* among host species (Tukey-type multiple comparisons test among proportions, $P < 0.05$). Sample size (n) refers to the total number of individuals sampled for each phorophyte species.

Species	Individuals/ha (Mean $\pm$ S.D.)	Percentage of individuals supporting <i>T. recurvata</i>
<i>Acacia</i> spp.	3.3 $\pm$ 8.2	100.0 ^{not tested} (n = 8)
<i>Aloysia lycioides</i> Cham.	73.3 $\pm$ 113.4	87.7 ^a (n = 81)
<i>Castela texana</i> (Torr. & A.Gray) Rose	10.0 $\pm$ 15.5	60.9 ^b (n = 23)
<i>Celtis pallida</i> Torr.	60.0 $\pm$ 75.9	96.6 ^a (n = 87)
<i>Cylindropuntia imbricata</i> (Haw.) F.M.Knuth	18.3 $\pm$ 24.8	97.0 ^a (n = 33)
<i>Bursera</i> sp.	3.3 $\pm$ 8.2	100.0 ^{not tested} (n = 2)
<i>Koeberlinia spinosa</i> Zucc.	6.7 $\pm$ 8.2	48.5 ^b (n = 33)
<i>Larrea tridentata</i>	166.7 $\pm$ 213.1	41.6 ^b (n = 178)
<i>Myrtillocactus geometrizans</i> (Mart. ex Pfeiff.) Console	5.0 $\pm$ 8.4	85.7 ^{ab} (n = 28)
<i>Opuntia</i> sp.	91.7 $\pm$ 121.4	89.3 ^a (n = 121)
<i>Prosopis laevigata</i>	191.7 $\pm$ 224.1	100.0 ^{not tested} (n = 115)
<i>Verbesina lindenii</i> (Sch.Bip.) S.F.Blake	1.7 $\pm$ 4.1	100.0 ^{not tested} (n = 1)
<i>Yucca</i> spp.	21.7 $\pm$ 24.0	41.3 ^b (n = 80)

Table 3 – Number of *Prosopis laevigata* individuals found in thirteen study sites in the Mexican Chihuahuan Desert.

The number in each cell is the number of *P. laevigata* corresponding to categories of height and *Tillandsia recurvata* cover index. Numbers in parentheses denote the number of *P. laevigata* individuals sampled to determine *T. recurvata* biomass.

Height	Ball moss cover index									Total
	0	1	2	3	4	5	6	7	8	
< 1 m	119 (0)	14 (1)	11 (1)	3 (1)						147
1.1–2 m	71 (0)	52 (1)	56 (1)	45 (1)	3 (1)	2 (1)				229
2.1–3 m	62 (0)	40 (1)	53 (1)	92 (3)	22 (1)	9 (1)	8 (1)	2 (1)	1 (1)	289
3.1–4 m	53 (0)	56 (1)	55 (1)	37 (2)	35 (1)	36 (1)	15 (1)	4 (1)		291
4.1–5 m	5 (0)	20 (1)	30 (1)	19 (1)	32 (1)	30 (1)	19 (1)	2 (1)		157
5.1–6 m			2 (0)	4 (1)	11 (1)	5 (1)	10 (1)	2 (1)		34
6.1–7 m					3 (1)	1 (0)	3 (2)			7
> 7 m						1 (0)				1
Total	310	182	207	200	106	84	55	10	1	1155

random sampling procedure (Schaeffer et al. 1986, Hofstede et al. 2001).

In the second step, with the estimate of *Tillandsia recurvata* biomass of each tree, we fitted a multiple regression model for the prediction of *T. recurvata* biomass in *Prosopis laevigata*. In this model, the dependent variable was biomass (kg), and the *Prosopis laevigata* independent variables were: height (m), maximum crown diameter (m), minimum crown

diameter (m), mean crown diameter (m), crown cover (m², calculated as the projection of a ellipse with the two perpendicular diameters measured), number of stems, maximum diameter of the stems (cm), stem basal area (cm²), bark area and *T. recurvata* cover index. Model construction was conducted with a forward stepwise routine (Fox et al. 1994). To resolve problems of multicollinearity, homogeneity of variance and normality of residuals (Zar 2010), certain variables were either transformed or removed from the analysis.

The bark area of each *Prosopis laevigata* was calculated with the formula: $\text{Log}_{10}[\text{Bark area (m}^2\text{)}] = -0.251 + 2.084 \text{Log}_{10}[\text{maximum diameter of the crown (m)}]$. This formula resulted from a multiple regression analysis similar to that explained previously. In this analysis maximum diameter of the crown was the only variable that explained bark area ($f = 466.9$, $p < 0.0001$, $r^2 = 0.93$) and no other *P. laevigata* variable significantly increased the power of prediction ($t < 2$) or, if so, problems of multicollinearity (e.g. mean crown cover) were incurred.

Finally, *Tillandsia recurvata* biomass was calculated for each transect. In this procedure, using the regression model described previously, we first estimated *T. recurvata* biomass for each *Prosopis laevigata* sampled and then pooled the estimated biomass of all the *P. laevigata* sampled in each transect. Values of *T. recurvata* biomass per transect were converted to kg/ha.

Vertical distribution of *Tillandsia recurvata* in *Prosopis laevigata* – To test for differences in the vertical distribution of *Tillandsia recurvata* in the strata of *Prosopis laevigata*, the observed biomass was divided by the bark area found in each stratum, thus controlling the effect of different substrate abundance (bark area) among strata. To test for differences in *T. recurvata* biomass between strata, we used an ANOVA model for a randomized block experimental design (Zar 2010). In this test, the fixed factor was the stratum (trunk, inner branches and outer branches), the random factor was the tree (each one of the 41 sampled *Prosopis laevigata*) and the response variable was biomass per unit of bark area. The same model was used to test for differences between strata with the raw data of biomass and bark area.

RESULTS

In the thirteen study sites, *Tillandsia recurvata* was found on 73% of the 1155 *Prosopis laevigata* individuals surveyed (table 3), being absent on the smallest (table 3), and no other holoeipiphyte was found. However, we found the following cacti growing accidentally as epiphytes: *Cylindropuntia leptocaulis* (DC.) F.M.Knuth (3 cactus individuals/3 *P. laevigata* individuals), *Echinocereus pentalophus* (DC.) Lem. (50 cactus individuals/34 *P. laevigata* individuals), *Ferocactus hirtix* (DC.) G.E.Linds. (16 cactus individuals/14 *P. laevigata* individuals), *Mammillaria crinita* DC. (7 cactus individuals/3 *P. laevigata* individuals), *M. magnimamma* Haw. (22 cactus individuals/15 *P. laevigata* individuals) and *Opuntia* spp. (22 cactus individuals/15 *P. laevigata* individuals).

Phorophyte preference

Independent of phorophyte species, *T. recurvata* was present in $74.2 \pm 35.9\%$ (hereafter mean $\pm$ S.D.) of the phorophyte individuals taller than 1.7 m in height in each transect; however, this frequency varied between study sites. In one site (Coyote, table 1), the percentage of phorophyte individuals hosting *T. recurvata* ranged from 5% to 15% while in another (Cerritos, table 1), the frequency was between 67% and

76% and between 84% and 100% in the remaining areas. Although *T. recurvata* inhabited all the scrubland phorophyte species greater than 1.7 m height (table 2), its frequency differed between phorophyte species ($\chi^2 = 180.5$, $p < 0.00001$): in *Aloysia lycioides* Cham., *Celtis pallida* Torr., *Cylindropuntia imbricata* (Haw.) F.M.Knuth and *Opuntia* sp., *T. recurvata* frequency was higher than 87%, while in *Castela texana* (Torr. & A.Gray) Rose, *Koeberlinia spinosa* Zucc., *Larrea tridentata* and *Yucca* spp., the frequency was between 40% and 60%. The phorophyte species *Acacia* spp., *Bursera* sp. and *Verbesina lindenii* S.F.Blake were excluded from the analysis because we found low abundance of individuals in the sample. However, all these species, along with the *Prosopis laevigata* trees taller than 1.7 m in this subsample, had a 100% incidence of *T. recurvata* (table 2).

Abundance of *Tillandsia recurvata* on *Prosopis laevigata*

The best predictors of *Tillandsia recurvata* dry biomass in *Prosopis laevigata* were: *P. laevigata* height and *T. recurvata* cover index ($f = 54.8$, $p < 0.0001$, $r^2 = 0.74$). *Tillandsia recurvata* dry biomass on *P. laevigata* could be predicted with the formula:

$\sqrt{\text{Biomass (kg)}} = -0.768 + 0.381 * P. laevigata \text{ height (m)} + 0.164 * T. recurvata \text{ cover index}$ (fig. 2). No other measured variable, even that of *P. laevigata* bark area, added a significant power of prediction for *T. recurvata* biomass (all $t < 1.5$, $p > 0.05$). Dry biomass of *T. recurvata* ranged from 0 kg to 9.4 kg per tree, with a mean of 0.35 ± 0.80 kg per tree.

Estimated dry biomass of *T. recurvata* in the scrubland ranged from 8.3 ± 18.4 kg/ha to 491.9 ± 92.3 kg/ha among the thirteen sampled sites ($n = 5$ transects per site), with an overall mean value of 124.1 ± 137.8 kg/ha for the whole area.

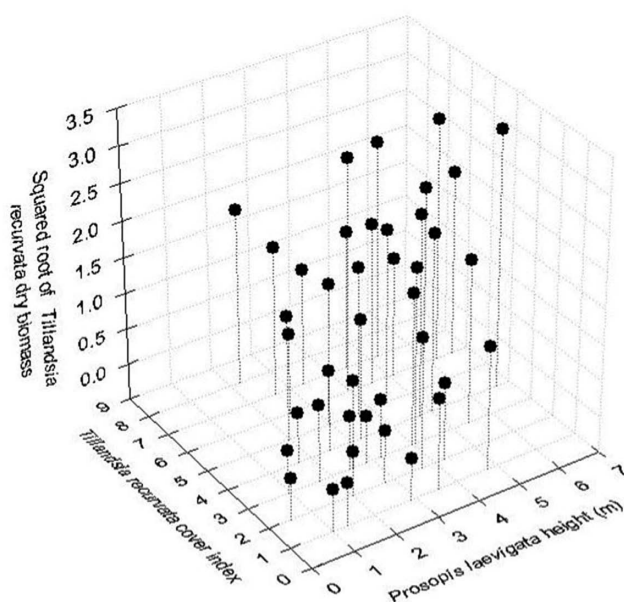


Figure 2 – Relationship between height, *Tillandsia recurvata* cover index and dry biomass of *T. recurvata* found in 41 *Prosopis laevigata* individuals sampled in the scrubland of the Mexican Chihuahuan Desert.

Vertical distribution of *Tillandsia recurvata* in *Prosopis laevigata*

Bark area differed between vertical strata of *Prosopis laevigata* ($f = 19.2$, $p < 0.0001$; fig. 3A). The majority of bark area was located in the outer branches ($65.9\% \pm 13.0\%$), while the inner branches accounted for $21.8\% \pm 10.1\%$ and the trunk comprised $12.3\% \pm 6.6\%$ of the total bark area (fig. 3A). The dry biomass of *Tillandsia recurvata* followed a similar pattern to that of bark area, differing between vertical

strata of the *P. laevigata* ($f = 25.0$, $p < 0.0001$; fig. 3B). Dry *T. recurvata* biomass was concentrated in the outer branches ($73.6\% \pm 21.1\%$), while the inner branches supported $24.5\% \pm 19.9\%$ and on the trunk there was only $1.9\% \pm 3.7\%$ (fig. 3B). However, this pattern was not consistent when we tested biomass per unit of area of bark (fig. 3C): this value differed between strata ($f = 19.2$, $p < 0.0001$), but outer branches (15.1 ± 15.7 gr/m² of bark) did not support more *T. recurvata* biomass than inner branches (12.2 ± 13.6 gr/m² of bark) (Tukey test $p > 0.05$). In this case, the trunk strata (0.8 ± 1.4 gr/m² of bark) supported significantly less *T. recurvata* biomass than the other two strata (fig. 3C).

DISCUSSION

We found only one species of holoeipiphyte. This met our expectation of low epiphyte richness in this semi-desert ecosystem. The studied scrubland is one of the poorest environments in terms of epiphyte species richness (see Wolf & Flamenco 2003) since in other semi-deserts of the tropical region there are more than one epiphyte species (e.g. García-Suárez et al. 2003).

The holoeipiphytic species found in this study inhabited all shrubs at a similar or greater frequency to that reported for epiphytes in humid habitats and in other semi-deserts. For example, all trees (DBH ≥ 20 cm) in a lower montane cloud forest of Veracruz, Mexico (1650 mm of precipitation and 118 epiphyte species) harbour epiphytes, and the most frequent bromeliad species are *Catopsis nutans* (Sw.) Griseb. (13–83% of frequency among all phorophyte species), *C. sessiliflora* (Ruiz & Pav.) Mez (19–91%), *Tillandsia butzii* Mez (57–79%), *T. kirchhoffiana* Wittm. (42–83%), *T. multicaulis* Steud. (50–89%), *T. punctulata* Schltdl. & Cham. (28–96%) and *T. viridiflora* (Beer) Baker (0–71%), which could be present in a maximum of 83–93% of trees (Flores-Palacios & García-Franco 2008). The other bromeliad species (eleven) were not as common, reaching maximum frequencies between 2% and 58% (Flores-Palacios & García-Franco 2008). In the semi-desert of the valley of Zapotitlan Salinas, Mexico, 92% of the phorophyte *Beauveria gracilis* Lem. and 83% of the phorophyte *Cephalocereus columna-trajani* (Karw. ex Pfeiff.) K. Schum. harboured *Tillandsia* spp. (García-Suárez et al. 2003); while *T. recurvata* was present in more than 40% of the individuals of the six phorophyte species (Bernal et al. 2005) and its frequency in another six phorophyte species drop to 30% or less. In the shrubs of this study, *T. recurvata* has a frequency similar to that of the most successful bromeliad epiphytes of a humid montane forest and semi-arid environments, and even when *T. recurvata* frequency differed between phorophyte species, the minimum frequency was still greater than 40%.

In other Mexican semi-desert tropical habitats, *Tillandsia recurvata* shows a distribution strongly biased towards a few phorophyte species, being more abundant in some (such as *Prosopis laevigata*) and less abundant in others (such as *Castela tortuosa* Liebm.; Bernal et al. 2005). A similar pattern occurs in a tropical dry forest (Vergara-Torres et al. 2010). The absence or low abundance of *T. recurvata* in some phorophyte species has been proposed as evidence of phorophyte limitation (Vergara-Torres et al. 2010) and ex-

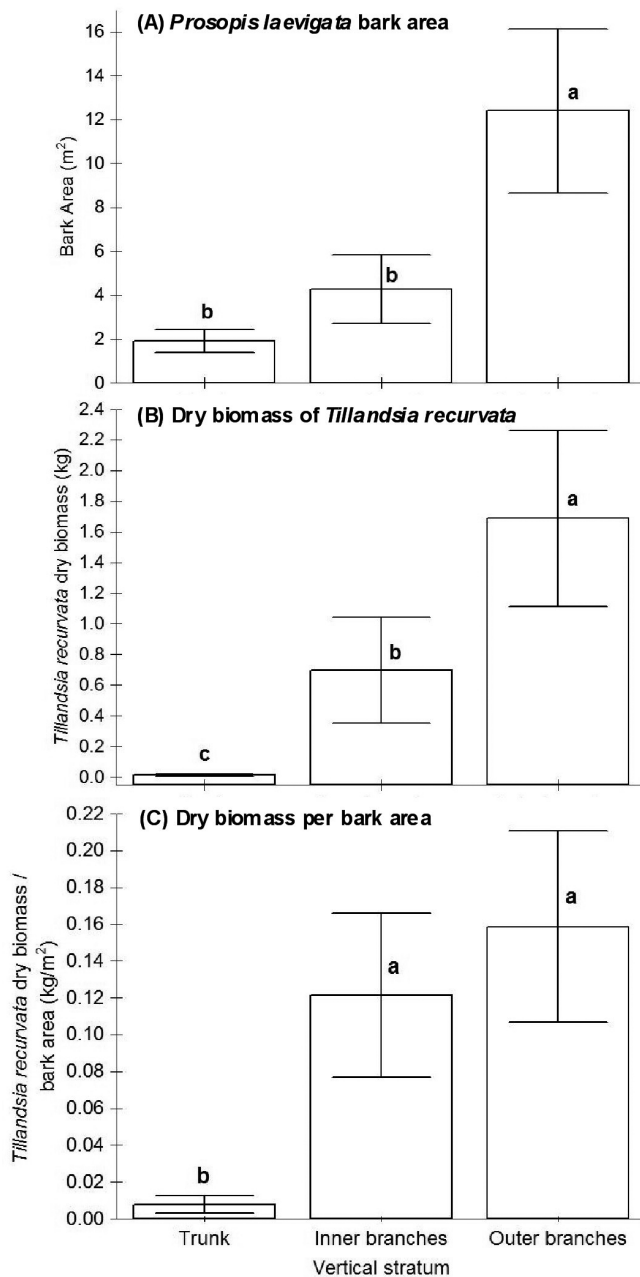


Figure 3 – Distribution of bark area and *Tillandsia recurvata* dry biomass in three vertical strata of *Prosopis laevigata*. Different letters indicate significant differences between means (Tukey test, $p < 0.05$). Bars represent 95% confidence intervals around the mean (column).

perimental evidence has shown allelopathic activity where extracts from the bark of trees that host few epiphytes actively reduce *T. recurvata* seed germination (Valencia-Díaz et al. 2010). As we only measured the frequency of *T. recurvata* between phorophyte species, we can not conclusively discard that some of these phorophytes are limiting species. In the semi-desert of the valley of Zapotitlan Salinas *T. recurvata* is highly frequent and abundant on *Acacia bilimekii* J.F. Macbr., *Parkinsonia praecox* (Ruiz & Pav. ex Hook.) Hawkins and *Prosopis laevigata*, but on *Mimosa adenanthroides* (M. Martens & Galeotti) Benth. is highly frequent but have a low abundance (Bernal et al. 2005), showing that frequency is not the best measure for testing phorophyte preferences and limitation among epiphytes. It is possible that some phorophyte species (e.g. *Koeberlinia spinosa*, *Yucca* spp.) in the area have characteristics that reduce *T. recurvata* colonization (e.g. small size, smooth bark), but it has a high frequency on this phorophyte species by a mass effect or vicinisms (Zonneveld 1995).

Tillandsia recurvata's biomass that we reported was highly variable, but in some sites it reached values similar to that found in humid montane forests (0.5 t/ha, see the review in Merwin et al. 2003). The studied scrubland can be considered as supporting a high *T. recurvata* biomass, because (a) the shrubs are smaller and could have less branches than the trees of the montane forests and thus support a smaller amount of epiphytes and (b), our estimate is based only on one phorophyte species. While *Prosopis laevigata* may be the dominant tree species in the studied scrubland (up to 63% of the individuals), other phorophyte species (e.g. *Acacia* spp.) could support similar biomass of epiphytes. For example, *Acacia* spp. in similar scrubland areas supports as many individuals of epiphytes as *P. laevigata* (Bernal et al. 2005). However, the contribution of *Acacia* spp. to the *T. recurvata* biomass of the scrubland was not considered in our survey.

The biomass of *Tillandsia recurvata* on *Prosopis laevigata* was a function of phorophyte height and *T. recurvata* cover index. Counterintuitively, the values of bark area did not predict the biomass of *T. recurvata*, but bark area itself could be predicted from only one measurement of the tree (crown diameter) as an allometric property. The relationship between the biomass of *T. recurvata* and tree height followed the recurrent pattern in which epiphyte abundance and richness is directly related to tree size (Flores-Palacios & García-Franco 2006). However, the significance of the *T. recurvata* cover index in the final equation was unexpected since this quantitative measure gives only a rough idea of epiphyte abundance. In the equation, the index probably functions as a correction for the high variance associated with epiphyte biomass estimation.

When testing if epiphytes prefer one vertical stratum, it is a normal procedure to test the number of individuals or the frequency of a species between strata (Johansson 1974), ignoring the fact that substrate abundance differs among strata (number of structures and bark area) (Zotz 1997). When we tested whether the biomass of *T. recurvata* and bark area differed between vertical strata, we found the same pattern for both variables: abundance increasing from the tree base to the outer branches. However, when we corrected the effect of bark area in the *T. recurvata* biomass, we found that

the abundance of this epiphyte was similar between branch strata, but lower on the trunk. Our data suggest that *T. recurvata* invades the branches of *P. laevigata*, as expected by the abundance of branches, but is unable to colonize the trunk. The scarcity of *T. recurvata* on trunks of *P. laevigata* could not be explained by dispersal limitation, since the trunk of even highly colonized phorophytes presented little or no *T. recurvata* individuals. In fact, *T. recurvata* seeds might not survive on the trunk of *P. laevigata* because over-shading from the crown reduced their photosynthetic capacity (Cervantes et al. 2005).

The high abundance of *T. recurvata* in the scrubland suggests that this epiphyte functions as a source of organic material and nutrients for the ecosystem. Epiphytes contain key elements such as P and N (Coxson & Nadkarni 1995, Flores-Palacios & García-Franco 2004) and, in forests where epiphytes reach a high biomass, it has been suggested that they enrich the forest with additional sources of nutrients (Nadkarni 1986). Moreover, *T. recurvata* harbours symbionts that fix atmospheric N (Puente & Bashan 1994). In the studied scrubland, the high *T. recurvata* biomass and its widespread distribution among phorophytes species and vertical strata, could influence the soil properties below the *P. laevigata* canopy by increasing shade, organic material and nutrients and thereby contribute to the creation of fertility islands (Gerner & Steinberger 1989, Olalde-Portugal et al. 2000).

Although *T. recurvata* could be beneficial for the ecosystem, its concentration on the branches may impact growth of *P. laevigata*, which concentrates growth and development of flowers on its branches. As a consequence, the high abundance of *T. recurvata* could interfere with the fitness of the tree, as has been suggested for some other phorophyte tree species colonized by *T. recurvata* (Montaña et al. 1997). Further research is required in order to fully elucidate this aspect of interaction between the two species.

This is the first study to document epiphyte abundance in the Chihuahuan Desert. *T. recurvata* was found to be highly abundant and frequent among phorophyte species and vertical strata, supporting the theoretical expectations that epiphytes can be highly frequent among the available substrate (Callaway et al. 2002). However, further research is needed in order to fully understand the role of *T. recurvata* in the studied scrubland, since it may be beneficial for the ecosystem but detrimental for its phorophytes.

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