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Habitat preference of the epiphyte *Tillandsia recurvata* (Bromeliaceae) in a semi-desert environment in Central Mexico

Rocío Bernal, Teresa Valverde, and Laura Hernández-Rosas

Abstract: *Tillandsia recurvata* L. is an atmospheric epiphyte that occupies tree canopies in many parts of tropical America. We investigated the host preferences of this species by analyzing its occurrence on trees in a 1-ha plot in a semi-desert environment in Mexico. Additionally, we carried out germination experiments and recorded seedling survival and growth in different microsites on the three preferred host species. Our results indicate that *T. recurvata* occupies the crowns of certain host species (*Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C. Harms, *Acacia bilimekii* Macbr., and *Cercidium praecox* (Ruiz & Pav.) Harms) with a higher frequency than expected by chance. In addition to species identity, tree size affected the probability of being occupied: small trees were occupied with lower frequencies and with lower densities than larger ones. On the other hand, distance to the nearest colonized tree was not related to the probability of a tree being occupied. Seed germination ranged from 0% to 7.5% and did not differ among the three host species tested. However, both seed germination and seedling growth were higher in the outer and upper parts of tree crowns. Given the patchy distribution of this epiphyte, we propose this system may be viewed as a metapopulation in which patch suitability varies according to host identity and size.

Key words: fragmented habitats, metapopulations, seed germination, seedling establishment, semi-arid environments, Tehuacan Valley.

Résumé : Le *Tillandsia recurvata* L. est un épiphyte atmosphérique, qui occupe la canopée arborée, dans plusieurs régions de l'Amérique tropicale. Les auteurs ont examiné la préférence des hôtes, chez cette espèce, en analysant sa présence sur les arbres dans une parcelle de 1 ha, dans un environnement semi désertique du Mexique. De plus, ils ont conduit des expériences de germination et enregistré la survie ainsi que la croissance des plantules, sur différents microsites, chez les trois hôtes préférés. Les résultats indiquent que le *T. recurvata* occupe les houppiers chez certains hôtes (*Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C. Harms, *Acacia bilimekii* Macbr., et *Cercidium praecox* (Ruiz & Pav.) Harms), avec une fréquence plus grande que celle provenant du hasard. En plus de l'identité des espèces, la dimension des arbres affecte la probabilité d'être habité; les petits arbres sont moins fréquemment occupés et portent une moindre densité que les plus grands. D'autre part, la distance par rapport à l'arbre voisin colonisé le plus près, n'est pas reliée à la probabilité qu'un arbre soit colonisé. La germination des graines va de 0 % à 7,5 %, et ne diffère pas entre les trois espèces d'arbre testées. Cependant, la germination des graines aussi bien que la croissance des plantules, sont plus élevées dans la partie supérieure et externe des houppiers. Compte tenu de la distribution de cet épiphyte, les auteurs proposent que ce système puisse être conçu comme une métapopulation, dans laquelle la convenance des colonies varie selon l'identité et la dimension de l'hôte.

Mots clés : habitats fragmentés, métapopulations, germination des graines, établissement des plantules, environnements semi-arides, vallée de Tehuacan.

[Traduit par la Rédaction]

Introduction

Vascular epiphytes are important elements of many tropical ecosystems; they are particularly abundant in tropical rain and cloud forests, although their presence in tropical dry forests and semi-arid shrublands is also common (Mondragón et al. 2004). Yet, little is known about the ecology of epiphytes; in particular, we lack knowledge about their spatial structure (Nieder et al. 2000) and their occupancy patterns of different habitat patches. In this study we focus on *Tillandsia recurvata* L., a bromeliad that inhabits the canopies of shrubs and trees in tropical semi-arid ecosystems in central Mexico (Rzedowski 1994; Montaña et al. 1997; García-Suárez et al. 2003). Although *T. recurvata* may establish on many host species (and even on inert substrates such as electricity cables), it is evident that not all trees in a community are occupied by this epiphyte to the same degree. In this paper we analyse the distribution of this species in a semi-desert shrubland and evaluate some factors that may be responsible for this distribution.

The naturally patchy distribution of epiphytes suggests that these plants may form metapopulations (sensu Levins 1969, 1970) restricted to patches (i.e., host trees or "phorophytes", sensu Benzing 1990) embedded in a matrix of less

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suitable habitat. In the case of *T. recurvata*, the individuals in each occupied tree may be considered as a local population within a larger metapopulation. These populations may vary in size, from a few to more than 300 individuals, depending on the size and species of the tree. Two features suggest that this system may be viewed as a metapopulation: (1) local populations are founded when dispersing seeds reach uncolonised trees and become extinct when colonized trees senesce and die, presumably persisting in a balance between colonization and extinction (Harrison 1991; Hanski 1999), and (2) seed dispersal (which occurs by wind) connects local populations together; however, as in other metapopulations, this connecting force appears rather weak because most dispersing seeds apparently remain within their original population and only a few (<0.6%, R. Bernal, unpublished data) reach other local populations. Our research group is presently conducting an extensive ecological study on this system, addressing aspects on demography, population genetics (using microsatellites), and seed dispersal in *T. recurvata*. Yet, some preliminary questions arose regarding the structure of this metapopulation system: what constitutes a colonizable patch for *T. recurvata* and are some microhabitats within the crown of host trees more successfully occupied than others? Regarding the first question, we hypothesize that *T. recurvata* does not perceive the habitat in strictly binary terms (i.e., colonizable habitat patches against non-colonizable habitat patches); rather, the different types of habitat patches (i.e., trees) must form a gradient, with some being more adequate than others for the establishment of local populations (Hanski and Simberloff 1997). This phenomenon, which strongly influences the spatial distribution of a species, has not been explored in depth among epiphytes, nor has it been addressed from a metapopulation perspective. In this sense, the characterization of the habitat patches that may be occupied by a species and a thorough understanding of the factors that influence their adequacy stand out as important ecological issues.

Several factors may help determine which patches (i.e., trees) are suitable for *T. recurvata*. Some kinds of trees may be more densely occupied than others because of differences in the probabilities of seed germination and seedling establishment under specific conditions. Benzing (1978, 1995) has reported that this species occurs excessively on thin branches. Additionally, the physical properties of host bark, as well as the presence of twisting branches, are important factors that affect establishment (Caldiz et al. 1993). Individuals of the genus *Tillandsia* avoid shady and (or) humid microsites (Benzing and Refrow 1971; Benzing 1990; Hietz 1997). All these factors acting together may result in *T. recurvata* plants occupying certain kinds of patches with higher frequencies than other patches and thus founding local populations on certain phorophytes. Also some microsites within phorophytes may be occupied more often than others (García-Suárez et al. 2003). These habitat preferences may be related to particular environmental factors that favour germination, establishment, and growth in some patches more than in others (Bazzaz 1991; Schupp 1995; Rey and Alcantara 2000).

By analysing the patterns of patch occupancy by *T. recurvata*, we aimed to identify the kind of habitat patches that are most hospitable to this species. In particular, we ex-

plored how the probability of a tree being occupied by *T. recurvata* is related to its identity, size, and distance to the nearest colonized neighbour (presumed to be the nearest source of colonists). In addition, we evaluated seed and seedling success within the crown of certain phorophytes. This study is the first step in an inquiry into the metapopulation dynamics of this epiphyte.

Materials and methods

Tillandsia recurvata

The genus *Tillandsia* includes some of the most drought-tolerant epiphytic bromeliads (Benzing and Refrow 1971; Benzing 1990; Hietz 1997). *Tillandsia recurvata* is an atmospheric epiphyte with a CAM metabolism (this type of photosynthetic metabolism seems to be restricted in the Tillandsioideae to the genus *Tillandsia*; Medina et al. 1977). Its distribution range includes tropical dry ecosystems from the southern Unites States to the middle part of Argentina, at altitudes from sea level to 3000 m (McVaugh 1992; Caldiz et al. 1993). The establishment of *T. recurvata* is influenced by the type of tree bark as well as the size and age of the branch (Caldiz et al. 1993; Harvey 1996). Plants possess a rudimentary root system that appears months after germination and is specialized as an attaching organ. Shoots are composed of 5–8 linear leaves; several shoots form a rosette-like semispherical structure. A terminal inflorecence, appearing in the autumn, completes the growth of the shoot (McVaugh 1992; Hietz and Hietz-Seifert 1994). Deeply embedded stamens and pistils suggest frequent autogamy, though apparently some cross-pollination is also carried out by the wind (Soltis et al. 1987). Capsules mature during the autumn and winter and release small plumose seeds (McVaugh 1992). Each fruit contains 57.62 ± 18.02 seeds ($N = 50$).

Study site

Field work was carried out in the Valley of Zapotitlan Salinas, in the Mexican state of Puebla (18°20′N, 97°28′W). This small valley forms a subsystem within the larger Tehuacan Valley, which is well known for its high cactus diversity and its overall floristic endemism (Hernández and Godínez 1994; Zavala-Hurtado and Díaz-Solis 1995; Beristain et al. 1996; Valiente-Banuet et al. 1997; Esparza-Olguín et al. 2002). The Valley of Zapotitlan Salinas has a sub-arid climate with mean annual temperatures oscillating between 18 and 22 °C (the minimum annual temperature is 11 °C and occurs in January; the maximum annual temperature is 34 °C and occurs in June). Annual precipitation fluctuates between 380 and 450 mm, most of which falls during the summer rainy season, between June and September. The vegetation at the study site is xerophytic shrubland dominated by columnar cacti (e.g., *Neobuxbaumia macrocephala, Neobuxbaumia tetezo, Cephalocereus columna-trajani, Myrtilocactus geometrizans*), globular cacti (i.e., *Mammilaria* sp., *Echinocactus* sp., *Ferocactus* sp.) and other characteristic elements such as *Agave macroacantha*, *Yucca periculosa*, *Lippia graveolens*, *Hechia podantha*, and *Beucarnea gracilis*. Thorny shrubs and trees that rarely exceed 3 m in height are common, for example, *Acacia coulteri*, *Acacia constricta*, *Acacia bilimekii*, *Mimosa adenanthoides*, *Proso-*

pis laevigata, *Cercidium praecox*, *Ipomoea arborescens*, *Kuebelinia speciosa*, and *Castela tortuosa* (Beristain et al. 1996; Montaña and Valiente-Banuet 1998). These elements, all of which correspond to native vegetation, act as nurse plants for many of the local succulents (Valiente-Banuet and Ezcurra 1991; Valiente-Banuet et al. 1997).

Data collection and analysis

In January 2001 we marked a 1-ha plot within the Zapotitlán Salinas Valley, near the village of Colonia San Martín. This plot was divided into 25 20 m × 20 m subplots that were marked by a wooden pole at each corner and all the trees and shrubs within were sampled (henceforth referred to as "trees"). We recorded each tree's position (*x* and *y* coordinates within the 1-ha plot) and species identity. We also measured the height, as well as the length and width of the crown (as if projected on the ground). From these data we derived a measure of tree size as the volume of an inverted cone (with an ellipsoid top). Tree size ranged from 0.001 to 44.3 m^3. The smallest woody plants corresponded to both naturally short-stature species and juveniles of larger-stature vegetation elements. We did not distinguish between the shrub and the tree lifeforms because they did not show a straightforward correspondence with species identity or size (i.e., many species may grow as both shrubs and trees; also large shrubby individuals, as well as very small tree-like plants, were found).

For each tree in the 1-ha plot, we counted the number of *T. recurvata* individuals anchored on its crown. With these data, we produced a map in which each tree could be located by coordinates, with an indication of its state of occupancy (i.e., occupied vs. unoccupied by *T. recurvata*). These data were used to address two main issues: (*i*) the probability of trees being occupied by *T. recurvata* and (*ii*) the intensity of colonization (i.e., the number of *T. recurvata* plants on occupied trees).

Probability of trees being occupied by T. recurvata

We analyzed the potential effect of three factors (tree species, tree size, and distance to the nearest source of colonists) on the probability of trees being occupied by *T. recurvata*. First, to test the effect of tree species, we calculated the proportion of trees of each species that were occupied by *T. recurvata*. Secondly, the effect of tree size on the probability of being occupied was analyzed by classifying trees into different size categories (irrespective of tree species) and evaluating the percentage of trees in each category that was colonized by *T. recurvata*. We also performed a correlation between the percentage of colonized trees per species and their average size (Table 1, last column). Finally, to analyze the effect of the distance to the nearest potential source of colonists, we used the *x,y* coordinates of each tree in the 1 ha plot to calculate the Euclidian distance to its nearest occupied neighbour. To make sure that the nearest occupied neighbour of all the analysed trees could be detected in the map of our 1-ha plot, we considered only those trees located within the central 90 m × 90 m subplot of our 1-ha plot. We calculated the average distance between both colonized and uncolonized trees to their nearest source of colonists and compared these average distances by means of a *t* test.

Intensity of colonization by T. recurvata

First, we wished to determine whether the *T. recurvata* plants found in the study plot (*N* = 14 324) were distributed among the different host species according to the availability of each of them (i.e., number of individuals per species or total crown volume per species) or whether *T. recurvata* had any preferences for certain host species. We nalyzed whether the number of *T. recurvata* plants established on each tree species differed from that expected by chance (according to their relative frequency or to the total crown volume offered, respectively) using χ^2 tests. In addition, we carried out a residuals analysis (Haberman 1973) to evaluate which tree species were used most heavily by *T. recurvata*.

We also evaluated the effect of host species identity, tree size, and distance to nearest occupied neighbour on the average number of *T. recurvata* plants per tree by means of a three-way ANOVA. The factor tree species had 12 levels (considering only those species represented by more than 15 individuals in the 1-ha plot; see Table 1); the factor tree size had seven levels (i.e., seven size categories, defined according to tree volume: 1, 0.001–0.05 m^3; 2, 0.05–0.5 m^3; 3, 0.5–2 m^3; 4, 2–8 m^3; 5, 8–15 m^3; 6, 15–30 m^3; 7, >30 m^3); and the factor distance to nearest occupied neighbour had five levels (i.e., five distance categories defined as: 1, 0–1 m; 2, 1–2 m; 3, 2–3 m; 4, 3–4 m; 5, >4 m). The response variable tested was the number of *T. recurvata* plants per tree (log transformed for linearity).

Seed germination and seedling establishment

Once the preferred host species were identified (i.e., those tree species that were occupied with a high frequency and were heavily infested), we performed seed germination experiments and recorded seedling survival and growth at different locations within the crowns of these tree species. According to coarse temperature and light measurements (results not shown), more external microsites within tree crowns are exposed to higher light intensity than internal microsites, while temperature varies in different parts of the crown depending on species identity (Hernández-Rosas 2003). For the seed germination experiments, four trees of each host species (i.e., *Prosopis laevigata*, *Cercidium praecox*, and *Acacia bilimekii*) were chosen. In each tree, six different microsites were distinguished within its crown, depending on the height (upper part and medium part of the crown) and the region (internal, intermediate, and external; see Fig. 1). In June 2002, we put 30 seeds in each microsite (attached to the branch by a small drop of Resistol 850 glue, which affected only the seed hairs). Germination was recorded monthly for 4 months.

In October 2001, after the rainy season had ended, we chose one tree representing each of the three host species mentioned above to follow the survival and growth of all the recently emerged *T. recurvata* seedlings. Most of these seedlings were clearly in very early stages of development (i.e., they were no more than swollen seeds), thus we could be sure that they emerged during the previous rainy season. Each seedling was marked by a tag attached to the branch next to it. Seedlings were monitored monthly for 11 months to record their survival and growth. Survival was evaluated as the presence or absence of previously recorded seedlings.

Table 1. Results of the sampling of *Tillandsia recurvata* in a 1-ha plot in the Zapotitlán Salinas Valley, Mexico.

Tree species	Tree density (individuals/ha)	% of trees*	Observed no. of *T. recurvata* plants	Expected no. of *T. recurvata* plants†	Haberman's residuals‡	% of *T. recurvata* plants§	Average size (m³)
Acacia constricta	280	24.1	1079	3460.5	–40.4	7.5	3.0
Mimosa adenanthoides	252	21.7	2712	3114.4	–7.2	18.9	3.4
Castela tortuosa	130	11.2	125	1606.6	–36.9	0.9	0.4
Prosopis laevigata	124	10.7	4713	1532.5	81.2	32.9	4.5
Acacia bilimekii	95	8.2	4289	1174.1	90.9	29.9	6.2
Kueberlinia speciosa	81	6.9	176	1001.7	–26.0	1.2	0.4
Calliandra eriophylla	66	5.7	41	815.6	–27.1	0.3	0.2
Agnondra obtusifolia	35	3.0	432	432.5	–0.02	3.0	1.0
Acacia cochliacantha	24	2.0	14	296.6	–16.4	0.09	0.4
Aeschinomene purpussi	18	1.5	0	222.4	–14.9	0	0.08
Cercidium praecox	18	1.5	506	222.4	19.0	3.5	5.1
Ipomoea arborescens	18	1.5	85	222.4	–9.2	0.6	5.4
Mimosa lacerata	7	0.6	42	86.5	–4.8	0.3	1.03
Eupatorium petiolare	4	0.3	22	49.4	–3.9	0.1	4.6
Acacia sericea	3	0.2	20	37.0	–2.8	0.1	13.2
Schaefferia stenophylla	2	0.1	61	24.7	7.3	0.4	4.9
Zizipus lloydi	1	0.1	7	12.3	1.5	0.05	—
Castella erecta	1	0.1	0	12.3	3.5	0	—
Total	1159	100	14 324	14 324		100	

*Percentage of each tree species, calculated from the total number of trees in the plot.

†Expected number of *T. recurvata* plants on each tree species, calculated according to their relative abundance.

‡Haberman's residuals = (observed – expected)/(expected)$^{0.5}$. Figures with absolute values >2 imply that differences between observed and expected frequencies are significant.

§Percentage of the total number of *T. recurvata* plants established on each tree species.

Fig. 1. Schematic representation of the different microsites within tree crowns. Region was either internal (IN), intermediate (IM), or external (E); height was either high (H) or medium (M).
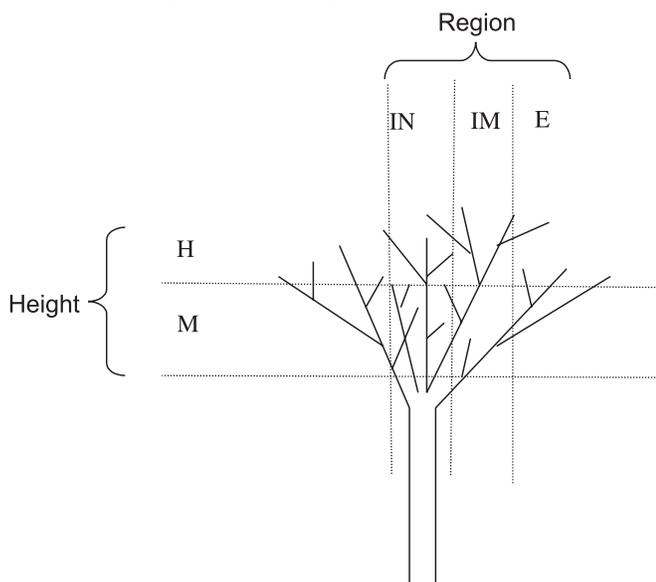
Growth was analysed in terms of the number of leaves produced per seedling over the 11-month period, as follows:

$$[1] \quad \frac{(\ln L_f - \ln L_i)}{t}$$

where L_f and L_i represent the final (in September 2002) and initial (in October 2001) number of leaves per seedling and

t is time (i.e., 11 months). This measure is intended to summarize the growth behaviour of seedlings over the 11-month period in relative terms, that is, in terms of the number of leaves per seedling at the end of the observation period, in relation to its initial number of leaves. Each seedling was assigned to one of six groups, depending on the microsite in which it was established (using the same microsite criteria discussed above; see Fig. 1).

A three-way ANOVA was performed to evaluate the effect of host identity, and height and region within the crown on seed germination (arcsin transformed to meet assumptions of normality). To analyze seedling growth, we carried out an ANOVA that tested the effect of height and region within the crown (both nested within "tree") on this response variable. In this case, the three trees (one *Prosopis*, one *Acacia* and one *Cercidium*) worked as replicates of the factor "tree"; we could not test the effect of "host identity" on seedling growth rate since we had only one tree per species. Finally, we performed a two-way ANOVA to evaluate the effect of height and region within the crown on seedling survival percentage (arcsin transformed). In this case, each tree was a replicate for each combination of height and region; again, the effect of host identity could not be evaluated because of the lack of replicates for this factor.

Results

Probability of trees being occupied by *T. recurvata*

Several tree species functioned as hosts for *T. recurvata* (Table 1). Of all the trees in our plot, 52% were occupied by the epiphyte. The most abundant tree was *Acacia constricta* (280 plants/ha). *Mimosa adenanthoides*, *Castella tor-*

tuosa, and *P. laevigata* were also among the most abundant (Table 1). However, not all tree species had the same probability of being occupied by the epiphyte. For instance, while 73% of *P. laevigata* trees were colonized, only 33% of *Castela tortuosa* supported *T. recurvata* plants (Fig. 2). *Acacia bilimekii* was also among the most abundant tree in the sampled hectare and a high proportion was occupied by *T. recurvata* (65%, Fig. 2). Although *Cercidium praecox* was represented by only 18 trees in our plot, more than two-thirds were occupied by *T. recurvata*. *Mimosa adenanthoides* and *Acacia constricta* also had high probabilities of being occupied (59.9% and 56.4%, respectively). Figure 2A shows that most colonized trees were relatively large (i.e., >0.5 m^3), while uncolonized trees belonged to the smallest size categories (Fig. 2B). In fact, the probability of being occupied increased with increasing tree size, irrespective of species identity (Fig. 3); trees of sizes 2–8 m^3 had nearly 80% probability of being occupied, and larger trees were occupied with a probability of almost 90% (Fig. 3). This suggests that an important aspect of the host–species preference was related to tree size. In fact, a highly significant correlation was observed between the percentage of colonized trees per species and their average size (Table 1; $r^2 = 0.552$, $F_{[1,12]} = 14.76$, $P = 0.002$). Tree species with an average short stature were occupied with lower frequencies than tree species with relatively larger average sizes.

Finally, we explored whether the probability of a tree being occupied by *T. recurvata* (irrespective of tree species and average size) was related to the distance to its nearest occupied neighbour. Within our 1-ha plot, ca. 52% of trees were occupied. The average distance between these occupied trees and their nearest occupied neighbour was 1.94 ± 1.29 m ($N = 372$), while the average distance between unoccupied trees and their nearest occupied neighbour was 2.06 ± 1.25 m (Table 2). These two means do not differ significantly ($t = 1.20$, df = 717, $P = 0.227$). Thus, we concluded that the distance to the nearest source of colonists didnot affect the probability of a tree being occupied by *T. recurvata* in our study plot.

Intensity of colonization by *T. recurvata*

The total number of *T. recurvata* plants recorded in the 1 ha plot was 14 324 (Table 1). These epiphytes were not distributed among the different tree species according to their relative frequency in the plot ($\chi^2 = 20\,276.30$, df = 11, $P < 0.0001$): of the 14 324 epiphytes, 33% were anchored on *P. laevigata* and 30% on *Acacia bilimekii* (Fig. 2B); thus, more than 60% of the *T. recurvata* plants were hosted by only two tree species. Yet, the individuals of these two species represented only 19% of the total number of trees in the sampled plot (Table 1). *Tillandsia recurvata* occupied the canopies of these species at much higher frequencies than expected by chance according to their relative frequency in the plot (Table 1); *Cercidium praecox* was also a heavily used host, despite its low density in the plot (Fig. 2B, Table 1). According to the residuals analysis (Haberman 1973), most of the other tree species were less heavily colonized by *T. recurvata* than expected by chance in relation to their relative frequency (e.g., *Acacia constricta*, *Castela tortuosa*, *K. speciosa*, and *Calliandra eriophylla*; Table 1). Except for *Acacia constricta*, these are all small

shrubs with average sizes below 0.5 m^3 (crown volume – average size given in Table 1) suggesting that, in addition to tree identity, size also affects the intensity of colonization by *T. recurvata*.

When we analyzed whether the number of *T. recurvata* plants anchored on each tree species was related to the total crown volume offered per species, we found, again, that the distribution of the epiphytes did not correspond to that expected by chance ($\chi^2 = 4122.37$, df = 11, $P < 0.0001$). While *Acacia bilimekii* and *P. laevigata* represented 19% and 17% of total tree volume in the 1-ha plot, respectively, the percentage of *T. recurvata* individuals established on these species was 30% and 33%, respectively (Table 1). Also, the proportion of *T. recurvata* individuals established on *Cercidium praecox* (3.5%) was higher than that expected by chance according to the proportion of the total crown volume offered by this species (2.9%).

The results of the ANOVA indicated that the number of *T. recurvata* plants per tree (log transformed for linearity) was significantly affected by tree species identity and tree size (Table 3). Additionally, these two variables showed a significant interaction, which means that the effect of tree size was not the same for all host species. On the other hand, the effect of distance to nearest occupied neighbour was not significant (Table 3). From the two variables that significantly affected the number of *T. recurvata* plants per tree, host species identity accounted for 25.2% of the variance, whereas tree size accounted for only 16.8% of the variance.

Seed germination and seedling survival and growth

Seed germination experiments performed on the three preferred host species showed that germination in the field was generally low. Mean germination percentages on different hosts and different microsites within tree crowns varied from 0.83% to 30% (Table 4). According to the results of the ANOVA performed to test the effect of host identity, region, and height on final germination percentage, the effect of host identity was not significant (df = 2, 54, $F = 2.06$, $P = 0.13$), neither was the effect of height within the crown (df = 1, 54, $F = 1.29$, $P = 0.26$). However, the effect of region was marginally significant (df = 2, 54, $F = 2.97$, $P = 0.059$). Slightly higher germination percentages were observed in the external part of the tree (Table 4).

Seedling survival percentages ranged from ca. 58 to 75 (Table 5). Seedling survival was not affected by height (df = 1, 12; $F = 0.78$; $P = 0.39$) or region (df = 2, 12; $F = 0.44$; $P = 0.65$) within tree crowns. However, we noticed that seedlings established on the *Acacia bilimekii* tree had a higher survival percentage (80.6%) than those established on *Cercidium praecox* (65.4%) or *P. laevigata* (45.9%). Yet, since we did not have replicates for host identity in this case, we could not test the significance of this effect.

Finally, seedling growth was significantly affected by "region" within the crown (df = 6, 410; $F = 8.20$, $P < 0.00001$); seedlings located in the external part of the crown grew faster than those in the intermediate or internal parts of the crown (Table 5). On the other hand, the effect of "height" within the crown did not have a significant effect on seedling growth (df = 3, 410; $F = 1.05$, $P = 0.37$). When we calculated the average growth rate of seedlings estab-

Fig. 2. (A) Relative frequency of trees of each species that were colonized by *Tillandsia recurvata*. (B) Relative frequency of trees of each species that were not colonized by *T. recurvata*. Only tree species with densities >10 individuals/ha are represented. Different shadings within columns refer to the relative frequencies of trees in different size categories.
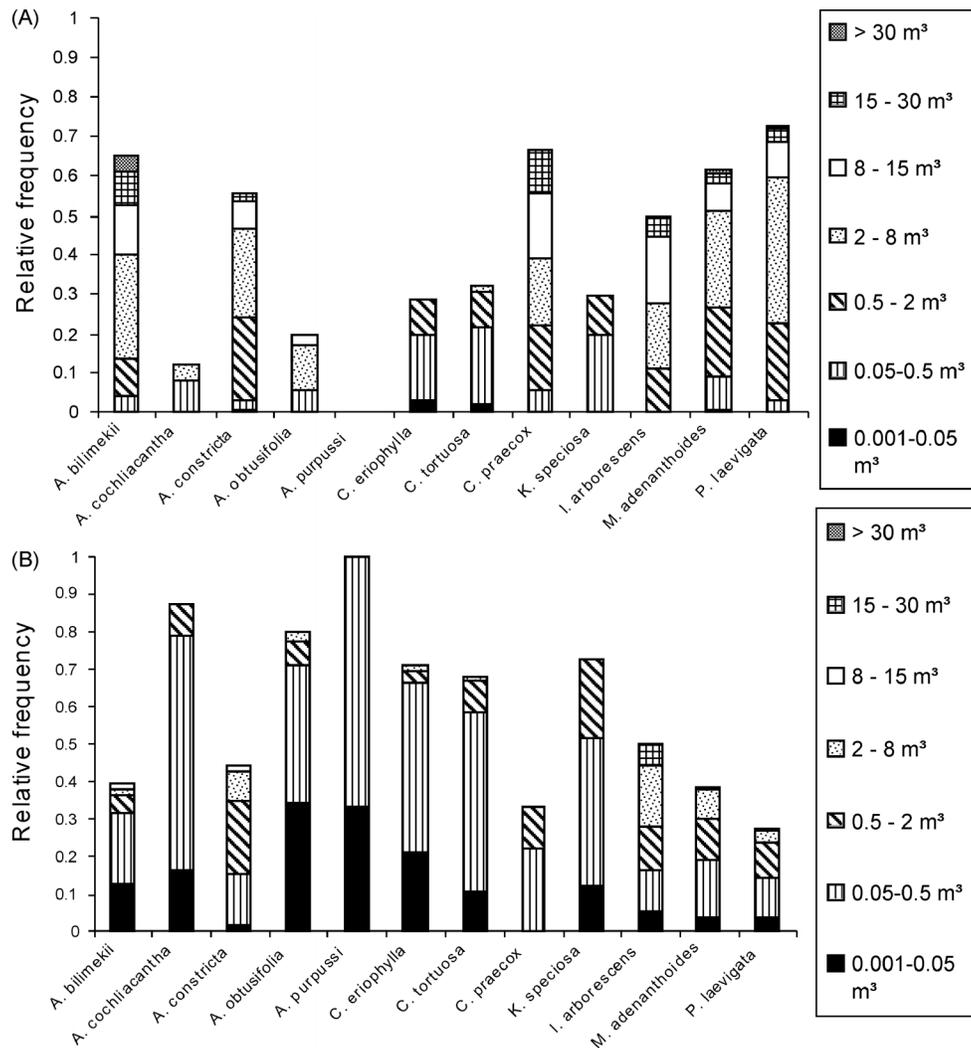
lished on the three different trees, we observed a slight tendency towards a higher growth rate in those established on *Acacia bilimekii* (0.058 leaves/leaf/month) and *P. laevigata* (0.053 leaves/leaf/month), compared with those established on *Cercidium praecox* (0.045 leaves/leaf/month); however, we could not test the significance of this effect since we did not have replicates for the factor host species.

Finally the effect of host identity on seedling growth was marginally significant ($F = 2.55$, $P = 0.078$), with a tendency towards a higher growth rate for seedlings established on *P. laevigata* (Table 6).

Discussion

The aim of this study was to explore the hypothesis that *T. recurvata* establishes more successfully on particular host species and in specific microsites within host crowns. Although at first sight this epiphyte appears to exhibit a random distribution (García-Suárez et al. 2003), our results indicate over-occurrence on some trees compared to others. Here we explored how host identity, size, and location rela-

tive to the nearest seed source affected the level of the use by *T. recurvata*. One of our more important findings was that *T. recurvata* plants do occupy certain hosts with a higher frequency than others, i.e., some patches are more suitable than others for housing local populations, and the adequacy of a patch is related to a large extent to its identity, and also to its size. This supports our initial suggestion that in this metapopulation patch suitability is not an all-or-nothing phenomenon in which the habitat may be characterized in binary terms, as has been assumed for most metapopulations (Hanski 1999). This finding, which surely is not exclusive to the *T. recurvata* system, calls for a re-evaluation of the traditional usage of the metapopulation concept and emphasizes that real metapopulations may be substantially more complex than initially envisaged. Although conceiving the landscape in binary terms may be adequate for the purpose of model simplification, when dealing with real metapopulations it is important to bear in mind that the specific features of habitat patches within the landscape (i.e., the composition of the tree community) may deeply affect metapopulation dynamics. For instance, in a tree

Fig. 3. Probability of trees of different size categories being colonized by *Tillandsia recurvata*. The values above each column represent the number of trees for which probabilities were calculated. Tree sizes were calculated as the volume of an inverted cone.
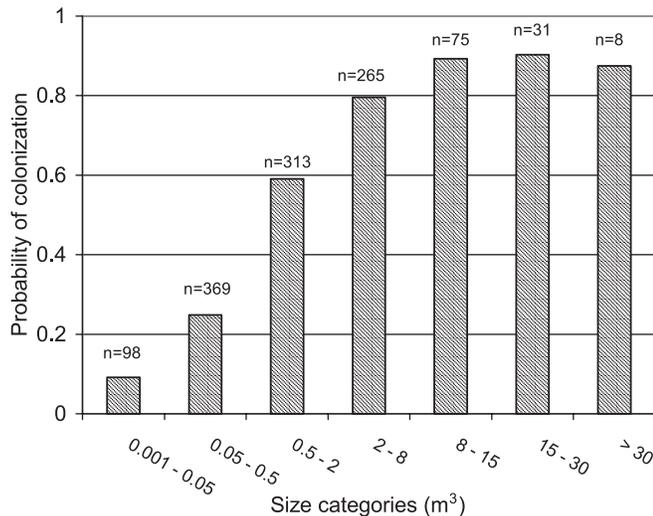
Table 2. Average distance between each focal tree (either colonized or uncolonized) and its occupied nearest neighbour.

State of focal tree	n	%	Distance (m)	Range (m)
Uncolonized	347	48.3	2.056	0.13–6.83
Colonized	372	51.7	1.94	0.25–7.74
Total	719			

community in which *P. laevigata* and *Acacia bilimekii* are conspicuous elements (which was the case in our 1-ha plot), *T. recurvata* will also be a prominent species. However, if the tree community is dominated by *M. adenanthoides* and *Acacia cochliacantha*, *T. recurvata* will be rather scarce because of the lack of suitable habitat patches. In fact, in our study area, it has been observed that the abundance of *T. recurvata* is related to the composition of the tree community at each particular site (García-Suárez et al. 2003).

Based on features such as the prevalence of colonization–extinction dynamics, in this study we have assumed that *T. recurvata* has a metapopulation structure. It remains to be tested, though, whether this epiphyte forms real metapopulations within which colonized trees actually function as local populations. A detailed survey of dispersal dynamics would be needed before making any conclusions. Our observations on seed dispersal indicate that most dispersed seeds remain within the source host tree, while only a very small percentage (<0.6%; R. Bernal, unpublished data) reach the crowns of neighbouring trees. Although maximum dispersal distances may allow wind-dispersed seeds to reach very remote places, it has been documented that most wind-dispersed seeds remain relatively close to their mother plant (Venable and Brown 1993; Chambers and MacMahon 1994). This appears to be the case for *T. recurvata*, whose seeds frequently disperse in clumps forming threads that adhere to the branches of the local host tree. Yet, the proportion of seeds reaching the crowns of neighbouring trees will depend, among other things, on the distance between neigh-

Table 3. Summary of the statistical results (ANOVA) of the effect of host species identity, tree size, and distance to nearest occupied neighbour on the number of *Tillandsia recurvata* plants per tree (log transformed).

Factor	F	P	df	Sum of squares
1. Host species	16.5	**0.0000**	10	27.7
2. Size category	18.3	**0.0000**	6	18.4
3. Distance category	0.81	0.5140	4	0.54
1 × 2	1.9	**0.0051**	26	8.4
1 × 3	1.2	0.2084	27	5.5
2 × 3	0.9	0.4660	16	2.6
1 × 2 × 3	0.8	0.6936	28	3.9
Residual			254	42.6
Total			371	109.9

Note: Statistically significant effects are given in bold.

Table 4. Average seed germination percentages of *Tillandsia recurvata* seeds sown on different host species and in different microsites within tree crowns.

Microsite	*Cercidium praecox*	*Acacia bilimekii*	*Prosopis laevigata*
M–E	5.00 (5.77)	3.33 (2.72)	30.00 (47.22)
M–IM	0.83 (1.67)	0.83 (1.67)	4.17 (6.31)
M–IN	2.50 (3.19)	2.50 (3.19)	3.33 (6.67)
H–E	10.83 (5.69)	5.00 (6.38)	10.00 (2.72)
H–IM	5.00 (4.30)	4.17 (6.31)	7.50 (6.87)
H–IN	3.33 (4.71)	11.67 (21.17)	7.50 (6.31)

Note: Nomenclature for microsites follows that presented in Fig. 1; the first letter refers to height within the crown, which can be either medium (M) or high (H), while the following letters refer to the region within the crown, which can be either external (E), intermediate (IM), or internal (IN). Mean germination percentages (and standard deviations) were calculated from four replicates of 30 seeds each (see Materials and methods).

bouring trees. The seed dispersal observations cited above were carried out at a site where trees are located ca. 10 m apart. In such landscape, colonized trees may in fact be functioning as rather independent populations within a metapopulation, linked by limited amounts of seed dispersal among them. However, in a landscape in which host trees are located very close to each other, groups of trees, rather than individual trees, may be functioning as local populations. In fact, in our 1-ha plot the average distance between trees was ca. 2 m; thus, at this level of clumping, trees may seldom be isolated enough to prevent colonization. This may explain our results with regards to the apparent irrelevance of the distance to the nearest colonized neighbour on the probability of a tree being occupied by *T. recurvata*. Presently we are developing molecular markers (i.e., microsatellites) from which a more detailed analysis of actual seed dispersal will be possible. So far, empirical evidence on the *T. recurvata* system at Zapotitlán highlights the fact that its spatial structure and functioning is far from straightforward.

In relation to host use, many epiphytes display some kind of habitat preferences (Benzing 1978, 1981*a*, 1981*b*). For instance, Benzing (1978, 1981*a*) found that *Tillandsia pauci-*

Table 5. Average relative growth rate of *Tillandsia recurvata* seedlings established in different microsites within the crowns of three trees and followed for 11 months.

Height or region	External		Intermediate		Internal	
	Mean (SD)*	*n*	Mean (SD)*	*n*	Mean (SD)*	*n*
Height	0.071 (0.056)	70	0.054 (0.046)	85	0.025 (0.038)	34
Medium	0.076 (0.043)	39	0.051 (0.042)	138	0.033 (0.036)	63

*Units are no. of leaves/leaf/month.

Table 6. Average survival percentage of *Tillandsia recurvata* seedlings established on different microsites within tree crowns.

Height or region	External	Intermediate	Internal
Height	63.13 (19.44)	75.28 (15.79)	66.09 (11.97)
Medium	57.69 (16.66)	63.30 (26.66)	58.37 (21.22)

Note: Seedlings were followed for 11 months (see sample sizes below). See Fig. 1 for an explanation of microsite characteristics. Averages (and standard deviations) for each microsite were obtained from three trees (one *Cercidium praecox*, one *Acacia bilimekii*, and one *Prosopis laevigata*). The initial number of seedlings from which survival percentages were calculated for each combination of height and region within the tree crowns were as follows: M–E = 10, 26, 35; M–IM = 56, 76, 94; M–IN = 6, 40, 61; H–E = 44, 44, 12; H–IM = 87, 13, 18; H–IN = 18, 9, 26 (microsite nomenclature follows that of Table 4).

flora and *T. recurvata*, in Florida, establish most frequently on *Taxodium distichum*, while Caldiz et al. (1993) reported that, in temperate forests at La Plata, Argentina, *T. recurvata* occurs in the crowns of *Cedrus deodara*, *Pinus radiata*, and *Celtis spinosa*. Also, *Tillandsia brachycaulos* establishes on *Gymnopodium floribundum* in the dry tropical forest of the Yucatan Peninsula (Mondragón et al. 1999; Mondragón et al. 2004), and *Tillandsia califanii* occurs mainly on *Beaucarnea gracilis* and *Cephalocereus columna trajani* (García-Suárez et al. 2003).

At our study site, we found that *T. recurvata*'s preferred host species were *P. laevigata*, *Acacia bilimekii*, and *Cercidium praecox*, according to the results of the χ^2 tests and Haberman's residuals. This preference could be accounted for, in part, by the rough surfaces that characterize the bark of these species. Conversely, *T. recurvata* was mostly absent on certain tree species, most of which possess smooth surfaces and (or) exceptionally thin branches (i.e., *Castella tortuosa*, *M. adenanthoides*, *Acacia constricta*, *K. speciosa*). Thus, trunk and branch characteristics (e.g., smoothness, diameter, presence of spines and other structures) could be major determinants of the establishment success of *T. recurvata* (Benzing 1990; Caldiz et al. 1993).

In addition to host identity, tree size was also shown to be an important factor affecting both the probability of being occupied and the intensity of colonization. Many of the tree species in which *T. recurvata* did not establish were small shrubs that rarely exceed 60 cm in height (i.e., *Calliandra eriophylla*, *Asechinomene purpussi*, *Castela tortuosa*, and *K. speciosa*), while preferred species are relatively large trees, sometimes reaching between 3 and 5 m in height. Within these preferred species, small trees were less heavily and less

frequently occupied than larger trees (data not shown). A potential explanation for this pattern is that large trees have been available for colonization for a longer time period than smaller ones (Yeaton and Gladstone 1982). An estimation of tree age would allow us to discriminate between the relevance of size and time available for colonization as potential explanatory variables for the observed occupancy patterns.

The preference towards large trees could also be related to their ability to capture dispersing seeds. Also, wind speed is generally higher in the upper parts of the canopy, thus crowns of large trees may be cooler and more ventilated than those of smaller trees (Hernández-Rosas 2003), which may create more adequate conditions for establishment. The results of our germination experiment support this view, since seed germination of *T. recurvata* was higher in the external parts of the crown than deeper within, and seedlings established in crown peripheries grew significantly faster than those located in intermediate or internal microsites; aeration might be important in this case since the outer parts of tree crowns are better ventilated than the inner ones. Light intensity may also be higher in the outer parts of tree crowns, which, in combination with greater air turbulence and the resulting lower temperatures, may favour seed germination and seedling growth. Atmospheric *Tillandsia* species require high radiation (Benzing 1981*b*, 1990). This may explain why *T. recurvata* seedlings established on *P. laevigata*, which is an evergreen tree, had higher mortality rates than those established on *Acacia bilimekii* or *Cercidium praecox*, which shed their leaves during the dry season (although the significance of this effect remains to be tested). Yet, a balance must be attained between the requirement for high radiation and the avoidance of the intense drought that prevails in highly illuminated microsites.

Tillandsia recurvata is one of the most common epiphytes in the neotropics. Yet, it is confined to certain habitat types and establishes only on certain host species. This species may reach a high abundance where the tree community is diverse and densely packed, as in our study plot, because of the availability of suitable habitat patches and the proximity among them, thus turning into a kind of epiphytic weed (Caldiz et al. 1993) or structural parasite (Montaña et al. 1997). Although habitat occupancy by epiphytes has been a much studied subject, it has seldom been evaluated from a metapopulation perspective. Here we present a first attempt to do so, which we believe deepens our understanding of the host–epiphyte relationship by offering insight into the way in which the dynamics and spatial structure of the landscape may determine the epiphytes' distribution and abundance. We are presently working on a demographic study of *T. recurvata* that will be of paramount importance to our under-

standing of the numerical behaviour of local populations established on host trees with different characteristics.

Acknowledgements

References

Bazzaz, F.A. 1991. Habitat selection in plants. Am. Nat. **137**(Suppl.): S116–S130. doi: 10.1086/285142.

Benzing, D.H. 1978. Germination and early establishment of *Tillandsia circinnata* Schlecht (Bromeliaceae) on some of its hosts and other support in Southern Florida. Selbyana, **5**: 95–106.

Benzing, D.H. 1981*a*. Bark surfaces and the origin and maintenance of diversity among angisoperm epiphytes: a hypothesis. Selbyana, **5**: 248–255.

Benzing, D.H. 1981*b*. The population dynamics of *Tillandsia circinnata* (Bromeliaceae): cypress crown colonies in southern Florida. Selbyana, **5**: 256–263.

Benzing, D.H. 1990. Vascular epiphytes. General biology and related biota. Cambridge University Press, Cambridge, UK.

Benzing, D.H. 1995. The physical mosaic and plant variety in forest canopies. Selbyana, **16**: 159–168.

Benzing, D.H., and Refrow, A. 1971. The significance of photosynthetic efficiency to habitat preference and phylogeny among Tillandsioid bromeliads. Bot. Gaz. **132**: 19–30. doi: 10.1086/336558.

Beristain, O.O., Valiente-Banuett, A., Dávila, P., and Medina, R. 1996. Tipos de vegetación y diversidad β en el Valle de Zapotitlán de las Salinas, Puebla, México. Bol. Soc. Bot. Mex. **59**: 35–58.

Caldiz, D.O., Belgrano, J., Fernández, V.L., and Andía, I. 1993. Survey of *Tillandsia recurvata* L. Preference, abundance and its significance for natural forests. For. Ecol. Manage. **57**: 161–168.

Chambers, J.C., and MacMahon, J.A. 1994. A day in the life of a seed. Movements and fates of a seeds and their implications for natural and managed systems. Annu. Rev. Ecol. Syst. **25**: 263–292. doi: 10.1146/annurev.es.25.110194.001403.

Esparza-Olguín, L., Valverde, T., and Vilchis-Anaya, E. 2002. Demographic analysis of a rare columnar cactus (*Neobuxbaumia macrocephala*) in the Tehuacan Valley, Mexico. Biol. Conserv. **103**: 349–359.

García-Suárez, M.D., Rico-Gray, V., and Serrano, H. 2003. Distribution and abundance of *Tillandsia* spp. (Bromeliaceae) in the Zapotitlán Valley, Puebla, México. Plant Ecol. **166**: 207–215.

Haberman, S.J. 1973. The analysis of residuals in cross-classified tables. Biometrics, **29**: 205–220.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, New York.

Hanski, I., and Simberloff, D. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. *In* Metapopulation biology. Ecology, genetics, and evolution. *Edited by* I. Hanski. Academic Press, San Diego, Calif. pp. 5–26.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biol. J. Linn. Soc. **42**: 73–88.

Harvey, C.A. 1996. Patterns of seed colonization and seedling establishment of ball moss (*Tillandsia recurvata*) on sand live oak trees (*Quercus germinata*) in Central Florida. Biol. Sci. **2**: 76–81.

Hernández, H.M., and Godínez, A.H. 1994. Contribución al conocimiento de las cactáceas mexicanas amenazadas. Acta Soc. Bot. Mex. **26**: 33–52.

Hernández-Rosas, L. 2003. Patrón de germinación y establecimiento de plántulas de *Tillandsia recurvata*: una contribución al estudio de su dinámica metapoblacional. B.Sc. thesis, Sciences Faculty, National Autonomous University of Mexico, Mexico City, Mexico.

Hietz, P. 1997. Population dynamics of epiphytes in a Mexican humid montane forest. J. Ecol. **85**: 767–775.

Hietz, P., and Hietz-Seifert, U. 1994. Epífitas de Veracruz. Guía ilustrada para las regiones de Xalapa y Los Tuxtlas, Veracruz. Instituto de Ecología A.C., Veracruz, México.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull. Entomol. Soc. Am. **15**: 237–240.

Levins, R. 1970. Extinction. Lect. Math. Life Sci. **2**: 75–106.

McVaugh, R. 1992. Flora Novo Galiciana. A descriptive account of the vascular plants of western Mexico. Vol. 15. Bromeliaceae. University of Michigan Herbarium, Ann Arbor, Mich.

Medina, E., Delgado, M., Troughton, J.H., and Medina, J.D. 1977. Physiological ecology of CO_2 fixation in Bromeliacae. Flora, **166**: 137–152.

Mondragón, D., Durán, R., Ramírez, I., and Olmsted, I. 1999. Population dynamics of *Tillandsia brachycaulos* Schltdl. (Bromeliaceae) in Dzibilchaltun National Park, Yucatán. Selbyana, **20**: 250–255.

Mondragón, D., Durán, R., Ramírez, I., and Valverde, T. 2004. Temporal variation in the demography of the clonal epiphyte *Tillandsia brachycaulos* (Bromeliaceae) in the Yucatan Peninsula, México. J. Trop. Ecol. **20**: 1–11.

Montaña, C., Dirzo, R., and Flores, A. 1997. Structural parasitism of an epiphytic Bromeliad upon *Cercidium praecox* in an Intertropical Semiarid Ecosystem. Biotropica, **29**: 517–521.

Montaña, C., and Valiente-Banuet, A. 1998. Floristic and life-form diversity along an altitudinal gradient in an intertropical semiarid Mexican region. Southwest. Nat. **43**: 25–39.

Nieder, J., Engwald, S., Klawun, M., and Barthlott, W. 2000. Spatial distribution of vascular epiphytes (including Hemiepiphytes) in a lowland Amazonian Rain Forest (Suromoni Crane Plot) of Southern Venezuela. Biotropica, **32**: 385–396.

Rey, P.-J., and Alcantara, J.M. 2000. Recruitment dynamics of a fleshy-fruited plant (*Olea europea*): connecting patterns of seed dispersal to seedling establishment. J. Ecol. **88**: 622–633. doi: 10.1046/j.1365-2745.2000.00472.x.

Rzedowski, J. 1994. La Vegetación de México. Limusa. México.

Schupp, W.E. 1995. Seed-patterns conflicts, habitat choice, and patterns of plant recruitment. Am. J. Bot. **82**: 399–409.

Soltis, E.D., Gilmartin, J.A., Rieseberg, L., and Gardner, S. 1987. Genetic variation in the epiphytes *Tillandsia ionantha* and *T. recurvata* (Bromeliaceae). Am. J. Bot. **74**: 531–537.

Valiente-Banuet, A., and Ezcurra, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, México. J. Ecol. **79**: 961–971.

Valiente-Banuet, A., Rojas-Martínez, A., Arizmendi, M.C., and Dávila, P. 1997. Pollination biology of two columnar cacti (*Neubouxbaumia mezcalensis* and *Neobuxbaumia macrocephala*) in the Tehuacan Valley, central Mexico. Am. J. Bot. **84**: 452–455.

Venable, D.L., and Brown, J.S. 1993. The population-dynamic functions of seed dispersal. Vegetatio, **107/108**: 31–55.

Yeaton, R.I., and Gladstone, D.E. 1982. The patterns of colonization of epiophytes on calabash trees (*Crescentia alata* HBK.) in Guanacaste Province, Costa Rica. Biotropica, **14**: 137–140.

Zavala-Hurtado, J.A., and Díaz-Solis, A. 1995. Repair, growth, age and reproduction in the giant columnar cactus *Cehalocereus columnatrajani* (Kareinski ex. Pfeiffer) Schuman (Cactaceae). J. Arid Environ. **31**: 21–31. doi: 10.1006/jare.1995.0045.