Flora 209 (2014) 580–586

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.com/locate/flora

Experimental evidence of an increased leaf production in *Prosopis* after removal of epiphytes (*Tillandsia*)

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ARTICLE INFO

Article history:
Received 21 September 2013
Received in revised form 23 June 2014
Accepted 31 July 2014
Edited by Dr. Rainer Lösch.
Available online 3 September 2014

Keywords:
Chaco forest
Tillandsia
Epiphytes
Epiphytosis
Conservation

ABSTRACT

The production of new leaves of host trees can be affected by the presence of epiphytic species. This experimental study was planned to evaluate the effects on the mean number of new leaves produced by *Prosopis alba* considering the factors site-disturbance, different epiphytes loads, and the respective zones in the tree crown. The number of new leaves produced was counted manipulating branches with originally low and high loads of epiphytes at different crown zones, in 10 trees per site. The effect of manual removal of epiphytes on the leaf production of the hosts was analyzed by comparing branch responses in short and medium periods of time (i.e., 6 months and 3 years, respectively). There were no significant differences when comparing the number of new leaves produced in the sampled trees at sites with different human disturbance intensities. By contrast, significant differences were observed between both epiphytic loads treatments and when comparing tree crown zones. Experimental results showed a higher subsequent host leaf production (>100%) in branches where epiphytes were experimentally removed, in comparison with branches with high load of epiphytes The number of new leaves produced in branches with naturally low loads of the epiphytes was higher than 1000% compared to branches with high *Tillandsia* loads. Finally, a higher significant production of new leaves was observed in the bottom crown zone as compared with the middle and upper crown zones. Furthermore, this trend was confirmed considering a longer time-period (3 years) after experimental removal of epiphytes. A significant increase (>100%) was observed when comparing the production of new leaves between different periods after total epiphyte removal. In consequence, *Tillandsia* species could be considered as "structural parasites" of *Prosopis alba*.

Introduction

Forest fragmentation due to different human disturbances is an important driver of population dynamics and community structure (Didham et al., 2012). Many plants and animals have been shown to respond in different ways to modified landscapes (Collinge, 2009; Ewers and Didham, 2006; Hauck et al., 2012); for example, leaves of some trees can be affected by environmental conditions due to different levels of human disturbance (Pignata et al., 1999). Distribution and structure of trees is interacting also with the epiphytes colonizing on them. Data on the genetic structure of populations of *Tillandsia achyrostachys*, an endemic bromeliad of the tropical dry forests of Mexico, suggest that habitat fragmentation has reduced allelic richness and genetic diversity, and increased significant genetic differentiation between populations (González-Astorga et al., 2004). Some *Tillandsia* species are good biomonitors for different anthropogenic activities as vehicular emissions, industrial and agricultural activities (Bermudez et al., 2009; Pignata et al., 2002; Wannaz et al., 2006). In comparison, little is known about the way in which human disturbance can affect the diversity of epiphytes, particularly in dry forests (Werner and Gradstein, 2009), as those of the Chaco region, or how epiphyte occurrences and leaf production vary on the same host species across a gradient of disturbance.

Epiphytic plants of the genus *Tillandsia* (Bromeliaceae) have a wide distribution in the Americas and present great richness and abundance in tropical humid forests (Billings, 1904; Köster et al., 2009; Krömer et al., 2013; Werner and Gradstein, 2009), and they are also abundant in plant communities of arid and semiarid environments (Cascante et al., 2008; García-Franco and Rico-Gray, 1990; Montaña et al., 1997). These epiphytes do not derive nutrients from their hosts, since they obtain water and nutrients from air and abiotic substrate material through several morphological and physiological adaptations (Benzing, 1990, 2000; Laube and Zotz, 2003). Therefore, the interaction established between these

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http://dx.doi.org/10.1016/j.flora.2014.08.007
0367-2530/

epiphytes and their hosts is considered a commensalistic relationship (Benzing and Seeman, 1978; Sáyago et al., 2013) or a facilitative interaction system (Callaway et al., 2002). Nevertheless, some epiphytic species can act as "structural parasites" (Stevens, 1987) because they can cause adverse effects in the host tree, such as defoliation and branch-death (Benzing and Seeman, 1978; Benzing, 2008; Caldiz and Beltrano, 1989; Johansson, 1974; Ruinen, 1953). For this reason, Ruinen (1953) has proposed the term "epiphytosis" to refer to this kind of interaction. Some epiphyte species can produce mechanical damage, they compete for light and nutrients, or cause secondary effects such as an increased susceptibility to pathogen attack or any allelopathic activity (Benzing and Seeman, 1978; Caldiz and Fernández, 1995). Benzing and Seeman (1978) stated that *Tillandsia* species should be considered "nutritional pirates" of their hosts. Aguilar-Rodríguez et al. (2007) have studied the anatomical damages caused by the growth of *Tillandsia recurvata* on *Prosopis laevigata* branches. When this epiphyte has been vigorously attached for a long time to the host bark, the damage is deeper in the tissues, affecting the distribution of secondary xylem cells and reducing the number and diameter of vessels. Hosts present chemical effects of aqueous and organic bark extracts on seed germination of epiphytic *Tillandsia*, which determine differential epiphyte abundances according to the hosts through different allelochemical compounds (Valencia-Díaz et al., 2010).

Even when correlations of host-epiphyte interactions have been widely documented, field experiments in which epiphytes have been manipulated to examine host-specific interactions are rare (Callaway et al., 2002; Zotz and Vollrath, 2002). Furthermore, the effects of epiphyte presence upon biological attributes of host trees have been scantily studied (Montaña et al., 1997; Vergara-Torres, 2012). Already Billings (1904), in a detailed study of *Tillandsia usneoides*, stated that the cause of the popular belief in the parasitism of *Tillandsia* could be its preference for sunny exposures. This habit would tend to increase *Tillandsia* abundance on trees which do not have a dense shade or if the trees lost their leaves during the year. Billings (1904) recognized that these objections are not sufficient to explain a reduction in tree foliage that people so often ascribe to the presence of *Tillandsia*, and he suggested that this problem can only be answered satisfactorily by an experimental approach.

Epiphytes may experience tree crowns as a mosaic of suitable and unsuitable habitats. Some species of *Tillandsia* tend to be concentrated deeply within the canopy where plants grow on the main trunk and on the proximal portions of the main branches (Benzing and Seeman, 1978). Tree crowns can impose some constraints on germination and on the establishment of epiphytes, offering a fragmented patchy habitat (Benzing, 1990; López-Villalobos et al., 2008, and references therein). *Tillandsia* species have small, wind-dispersed seeds (Benzing, 2000); yet, the implications of spatial heterogeneity on germination and survival have rarely been studied in epiphytes (Winkler et al., 2005; Zotz and Vollrath, 2002). Bark characteristics and peeling rate may be important in determining the number and composition of epiphyte species that grow on a particular tree species (López-Villalobos et al., 2008). Zotz (1997) found a higher seedling survival in the tree periphery and stem base than on intermediate branches, but he did not find evidence for differential seedling mortality between growing sites when he studied the distribution of three epiphytic bromeliads. In addition, the distribution of older individuals was not related to that site-specific survival of seedlings (Zotz and Vollrath, 2002). Winkler et al. (2005) exposed seeds of five bromeliad species (four *Tillandsia*) to different canopy positions in a Mexican montane forest and they reported that there was no evidence that canopy position affected the probability of germination; yet, time to germination was shorter in less exposed canopy positions indicating that higher humidity accelerates germination. Host-specific availability of branch surfaces of different size for epiphyte establishment can also affect the abundance rates of the latter in different parts of the tree crowns (Ruiz-Cordova et al., 2014). However, it seems that to date no study has measured in detail the effects of epiphytes on host leaf production considering different crown zones.

The aim of this experimental study was to analyze the effects on the mean number of new leaves produced by *Prosopis alba* Griseb. according to (a) the level of disturbance of the sites, (b) the experimental treatments to evaluate the effect of the presence of different epiphyte loads, and (c) the crown zone in which the experimental treatments were performed. The effect of manual removal of epiphytes on the leaf production of the host at short and medium terms was also analyzed. Finally, based on the main results, management practices concerning atmospheric bromeliads on native host trees are discussed in the conservation context of the Chaco forests.

Materials and methods

Study area

The study was conducted in the Province of Córdoba (Argentina), within an altitudinal range between 400 and 700 m above sea level. The three sampling sites are located within the Chaco Domain, considering the phytogeographic categorization proposed by Cabrera (1971). This Domain is characterized by the presence of forests with a continuous canopy, immersed in agro-systems that are used with highly developed technology. In general, these forests show a predominance of deciduous woody, xerophytic species (Cabrera, 1971). Chaco Domain presents mild winters and warm summers, with an annual mean temperature of 18 °C, and a maximum mean temperature of 31 °C in January (the hottest month of the austral summer). The region presents a semi-dry climate with large water deficits and seasonal rainfalls (Capitanelli, 1979). The average annual rainfall in this area ranges between 600 and 800 mm; rainfalls are mainly concentrated during spring and summer (October–March). This region is characterized as semiarid due to the presence of a high potential evapotranspiration, which causes a water deficit throughout the year (i.e., 69 and 97 mm of water deficit during the wet and dry seasons, respectively). *Prosopis alba* was selected as the focal species of our study because it is a representative tree of semi-arid Chaco forests of central Argentina (Cabrera, 1971).

Intensity of human disturbance of the environment

Three sites with different levels of human disturbance were chosen, all located within the Chaco region. Human disturbance was determined qualitatively by considering the presence and number of buildings, highways or side roads, and the characteristics of the vegetation in the sampling area. Most of the epiphyte biomass living on host trees (*Prosopis alba*) belongs to *Tillandsia capillaris* (Astegiano et al., 2007). This species is considered a good biomonitor not only for different anthropogenic activities as pollution by heavy metals of both vehicular emissions and urban industrial activities, but also for agricultural activities (Bermudez et al., 2009; Pignata et al., 2002; Wannaz et al., 2006).

The three study sites were characterized according to their degree of human disturbance as follows:

Less intensity: This site presents an area of more than 1000 ha of continuous native forest, located near Río Ceballos city (Colón department, 31°10′ S, 64°10′ W). This area is mainly used for livestock production, and for agriculture to a lesser extent. This site presents well-conserved forests fragments, with numerous native

tree species of Chaco forests. No buildings or highways were registered within the sampling area.

Intermediate intensity: This area corresponds to Villa Los Aromos town, located in Santa María department (31°44′ S, 64°26′ W). At this site, *Prosopis alba* trees located in sidewalks, backyards, and uninhabited areas were sampled. Few buildings were recorded at this site (mainly family houses) and many side roads. Sampled trees were isolated in most of the cases and sometimes surrounded by exotic plants.

Higher intensity: This area corresponds to the Zoo park of Córdoba city (capital of the department, 31°25′ S, 64°10′ W). A high number of buildings and highways, and significant levels of ambient pollution near the sampled trees were registered in the surrounding area. This site also presents many woody exotic species.

Effect of different epiphytes loads on leaf production of Prosopisalba

Sections of branches on 30 individuals of *Prosopis alba* (10 trees at each site) were tagged between July and September 2006. Since these trees can reach from 5 to 12 m height, stairs, ropes and a harness were used to have access to the different crown sections (Fig. 1A). A total of 18 branch sections of 1 m length were tagged in each tree. Branches were chosen with a basal circumference of 10–15 cm, and distributed over the tree crowns of the hosts, according to a stratified random sampling. The crown was visually divided into three areas (bottom, middle and upper) in order to consider the variability that could be present in the community of epiphytes within the same host tree (Gradstein et al., 2003; Krömer et al., 2006; Ruiz-Cordova et al., 2014; San Martín et al., 2008; Winkler et al., 2005). Within each area, two separate zones of the crown were selected depending on the direction of the main bifurcation of the tree trunk (Fig. 1A). Three branch sections (if possible originated from the same limb) that contained different natural loads of epiphytes (i.e., two branches with high abundance and another without epiphytes or with negligible abundance; Fig. 1B) were selected in each crown zone. All the individuals of *Tillandsia* spp. present in one of the two branches with high abundance of epiphytes were manually removed to evaluate the short-term effect of epiphyte removal on the production of new leaves. This sampling criterion allowed us to consider branches with different epiphyte loads, but with similar age, area, and comparable colonization times. Three different situations were investigated: (1) sections of branches with naturally low epiphyte loads, (2) sections of branches with total removal of epiphytes that before have had a high abundance of *Tillandsia* spp., and (3) sections of branches with an un-changed naturally high abundance of *Tillandsia* spp. After six months, at the beginning of the summer season (January and February 2007), the number of new leaves produced on the branch segments assigned to each treatment was quantified. The leaves of *P. alba* are bi-pinnately compound, so always the whole leaf was considered in the counts and not the individual pinnae or pinnules. This response variable was chosen because the hosts are semi-deciduous trees, so it is possible to recognize easily the new leaves produced at the beginning of each season by their particular color and texture. In addition the number of new leaves is easy to quantify and represents a reliable estimator of the health status of trees. For that reason this variable has been used also in previous studies that evaluated the effect of *Tillandsia* epiphytes on their host trees (Benzing and Seeman, 1978; Montaña et al., 1997). The number of inflorescences and fruits produced in the selected branches were also quantified as a possible estimator of the epiphytes presence effect on host trees reproduction. However, the production of flowers and fruits was negligible in the three treatments, so that these variables were not further analyzed in this study.

Medium-term effects of Tillandsia removal

The number of new leaves produced in branches of 14 additional individuals of *Prosopis alba* was recorded after total *Tillandsia* removal from these focal hosts. They were cleaned out of *Tillandsia* epiphytes three years before data collection. The sampled trees were located in two semi-urbanized sites (intermediate intensity of disturbance), within the neighboring towns of Villa Los Aromos and La Bolsa. In each of these trees, four branch sections of 1 m were randomly selected. At each section, the number of new leaves produced was registered.

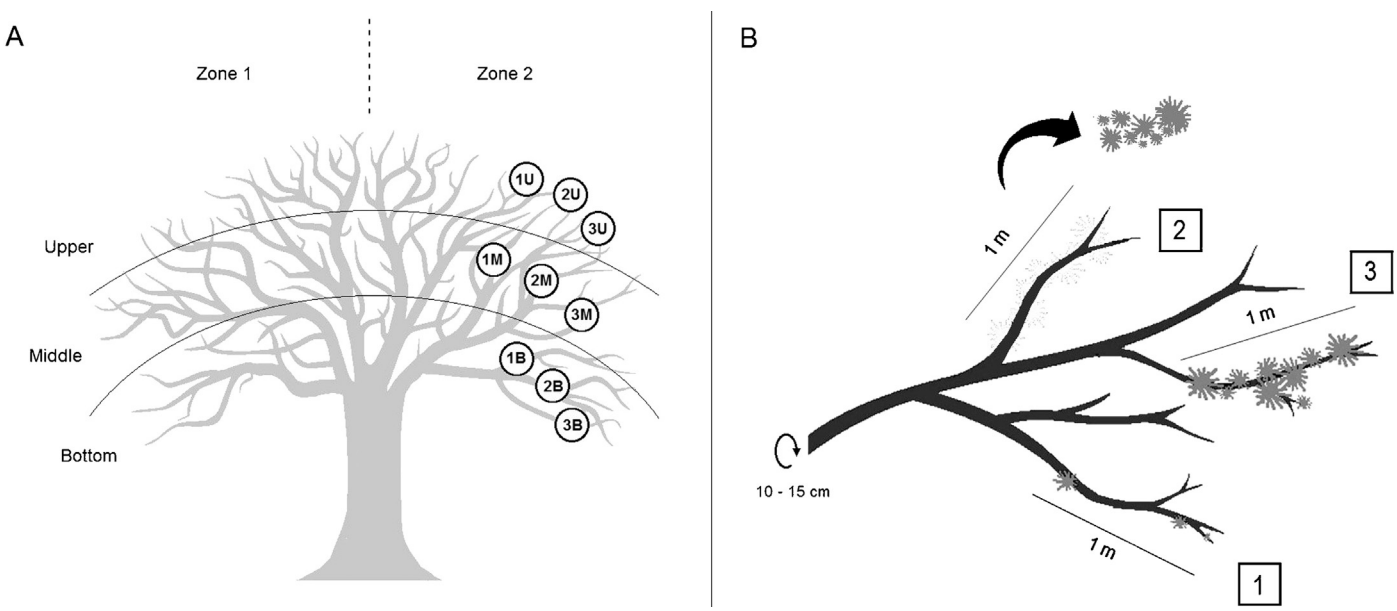

Fig. 1. (A) Schematic representation of the *Prosopis alba* tree crown zones (bottom, middle and upper). (B) Schematic representation of the branches (right) used for the different treatments performed in branch sections of 1 m length (1: naturally low epiphyte load; 2: total experimental removal of epiphytes with a previous high abundance of *Tillandsia* spp.; 3: naturally high abundance of *Tillandsia* spp.).

Table 1
Results of the different factors and interactions tested by GLMM using the mean number of new leaves produced per 1 m branch of 30 focal host trees (*Prosopis alba*). Factors are: "site" (sites with different intensities of human disturbance), "treatment" (experimental manipulation for *Tillandsia* epiphyte loads), and "zone" (regions within the host crown).

Term	Df	Deviance (χ^2)	*p*-Value
Site	2	2.36	0.3076
Treatment	2	2021.5	<0.0001
Zone	2	220.8	<0.0001
Site:zone	4	64.2	<0.0001
Treatment:zone	4	55.9	<0.0001
Site:treatment	4	85.7	<0.0001
Site:treatment:zone	8	48.8	<0.0001

Data analysis

Due to the non-normal distribution of the variable "number of new leaves" in most treatments, a generalized linear mixed model (GLMM) with a Poisson distribution was used for data analysis. The statistical model was run considering "treatments" and "site category" (according to their intensity of human disturbance) as fixed effects. Sampled trees, the crown zone (bottom, middle and upper), and the corresponding repetitions for each treatment (branches within tree) were considered as random effects. A GLMM was used to evaluate the variable "number of new leaves" when comparing the two periods of time (6 months and 3 years, respectively) after *Tillandsia* removal. Analyses were performed using the statistical programs R V-2.15.3 (R Core Development Team, 2013) and InfoStat (2012).

Results

Effects of experimental handling treatments of different epiphyte loads on the production of new leaves of Prosopisalba

Figure 2 shows the mean number of new leaves produced by *Prosopis alba* according to the level of disturbance of the sites, the presence of different epiphytes loads, and the crown zone in which the experimental treatments were performed. Table 1 shows the values of χ^2 with their respective probabilities, obtained from the GLMM analysis. There were no significant differences when comparing the mean number of new leaves produced at the sites with different human disturbance intensities (Table 1 and Fig. 2). By contrast, significant differences were observed with concern to both experimental removal treatments and the crown zone of the trees. There were statistically significant differences in the mean number of new leaves produced when comparing the experimental treatments with differences in *Tillandsia* loads (Table 1 and Fig. 2). The number of new leaves produced per 1 m branch was higher in those branches with naturally low load of epiphytes than in the other two treatments. The differences in the number of new leaves, when comparing branches with naturally low and high *Tillandsia* loads, were higher than 1000% (Fig. 2). Total *Tillandsia* removal treatment showed intermediate values, but with significant differences compared with the situation of high load of epiphytes that showed the lowest values of new leaves produced per 1 m branch. These results show a higher leaf production (>100%) after removal of epiphytes than in branches with naturally high loads of epiphytes. In addition, when comparing the different crown zones of the trees, independently of the experimental treatment, a significantly higher production of new leaves was observed in the bottom, compared with middle or upper zones of the trees (Fig. 2).

Effects of epiphyte removal on the production of new leaves of Prosopisalba after a longer period of time

The production of new leaves was higher after total epiphyte removal when comparing a medium period (three years) with a shorter one (6 months). The mean number of leaves produced per 1 m branch was 6 ± 4.5 and 2.3 ± 3.2, for the medium and shorter periods, respectively. These differences are significant ($p < 0.0005$) when data for these two periods are compared with a GLMM analysis (Poisson distribution for the data obtained after removals performed in 2004 and 2007).

Discussion

The absence of clear differences in the number of new leaves produced by *Prosopis alba* at the three sampling sites was suggestive because actually epiphytic and host species are often susceptible to variations of human disturbance (Bermudez et al., 2009; Pignata et al., 1999, 2002; Wannaz et al., 2006; Werner and Gradstein, 2009). But also previous studies in the tropical Andes have shown that species density of vascular epiphytes (species per tree) did not significantly differ among habitat types along a gradient of human disturbance, suggesting that dry forest communities of vascular epiphytes may be comparatively disturbance-resilient (Werner and Gradstein, 2009). In contrast, epiphytic cryptogams were sensitive indicators of microclimate and human disturbance in montane dry forests of Ecuador (Werner and Gradstein, 2009). Epiphytic lichen and *Tillandsia* communities that develop on particular host trees can differ in the direct and indirect host-*Tillandsia*-lichen interactions, as they are influenced by pollution and other human disturbances (Callaway et al., 2001). This is one possible explanation for the absence of general differences in the number of new leaves among trees. In consequence, new detailed studies on the balance of such relationships between *Prosopis* and epiphytic communities within the disturbance gradient are required.

Differences in leaf production among crown zones of *Prosopis alba*, independently of the *Tillandsia* loads, may be related to some characteristics of the tree. López-Villalobos et al. (2008) hypothesized that some tree species that have bark with low water-holding capacity, producing allelochemicals, or having a tendency to peel off, may carry fewer epiphyte species than those trees with bark that has a higher water-holding capacity, lacks allelochemicals or is a durable bark. They found that the peeling rate of *Bursera fagaroides* depends on branch size suggesting that *Tillandsia* distribution depends not only on peeling rate but also on seed dispersion (López-Villalobos et al., 2008; cf. also Ruiz-Cordova et al., 2014). Nevertheless, this source of variability was controlled in our experiments by selecting branches of similar diameter. Thus, other sources of variability would be influencing the process of leaf production among the tree crown zones. Zotz (1997) found that peeling rate varies inside the crown of *Annona glabra* and that *Tillandsia* seeds are differentially captured by the exterior twigs and branches of the host. Nevertheless, *Tillandsia* seeds that colonized the trunk showed the lowest probability of dying despite the high peeling rate, probably because of better microclimatic conditions on the trunk compared with upper crown zones (Zotz, 1997). Winkler et al. (2005) found that there is no evidence that canopy position affects the probability of germination of *Tillandsia* seeds. Nevertheless, time to germination was shorter in less exposed canopy positions indicating that higher humidity accelerates germination (Winkler et al., 2005). It is possible that these differences in the microclimatic conditions within the tree can be related to a differential leaf production between the crown zones.

The number of new leaves produced in branches of *Prosopis alba* with high loads of epiphytes was significantly lower compared to branches with epiphytes removed or with a naturally low load of

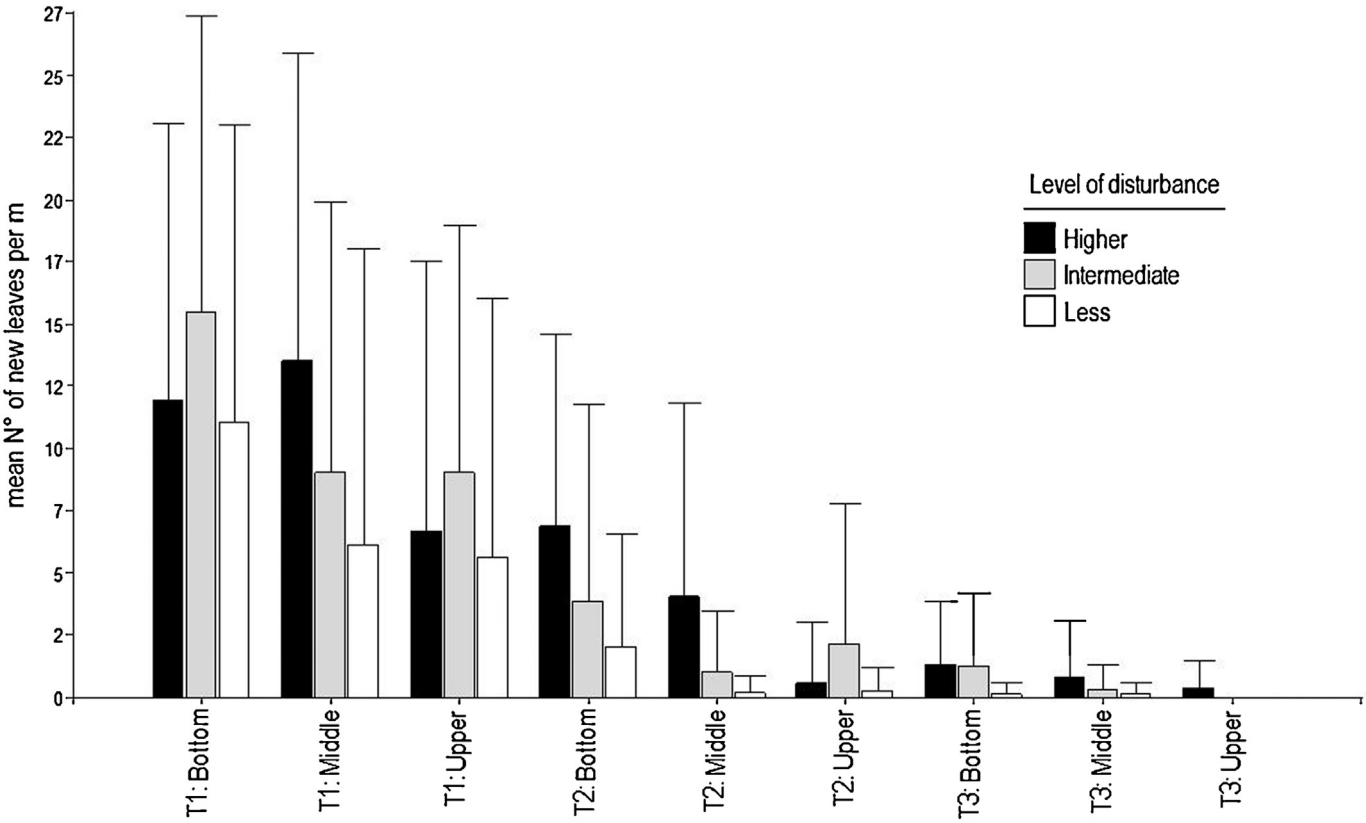

Fig. 2. Mean number of new leaves produced per branch section (1 m) of *Prosopis alba* at sites with different intensities of disturbance, with different situation resp. experimental treatments of *Tillandsia* epiphyte load and at different tree crown zones. Vertical bars show the mean and standard deviations of number of new leaves produced for the sampled branch sections. The different signatures of the bars correspond to the three study sites within the human disturbance gradient (black, gray, white for higher, intermediate and less, respectively). The bars were grouped by the experimental treatments (T1: branches with naturally low loads of epiphytes; T2: total removal of epiphytes in sections with high loads; T3: branch sections with naturally high loads of epiphytes) and indicating the tree crown zones where such treatments were applied (bottom, middle and upper sections of the crown, respectively).

epiphytes. These results might suggest the existence of some negative effects on the capacity of the host to produce new leaves caused by the presence of *Tillandsia* spp. This pattern is consistent with previous reports which document negative effects on some host tree species as a result of colonization by many epiphyte species (Benzing and Seeman, 1978; Caldiz and Beltrano, 1989; Johansson, 1974). Some *Tillandsia* spp. that could compete with their hosts for light and/or nutrients were described as "structural parasites" (Caldiz and Fernández, 1995). In a study conducted in Mexico, the presence of *Tillandsia* epiphyte species (*T. recurvata*) was linked with a reduced new leaf production in its host (*Cercidium praecox*), concluding that the presence of the epiphytes could negatively affect the leaf production and the photosynthetic capacity of their hosts (Montaña et al., 1997). Thus, considering the results obtained for this particular type of interaction between *Tillandsia* species and *Prosopis alba* trees, epiphytes act indeed as "structural parasites" for their hosts. This conclusion is supported by results showing that the number of new leaves is increased after experimental epiphytes removal, which suggests that the physical space occupied by the epiphytes ("primary interference") in the branches affects leaf production. Nevertheless, the positive effect on leaf production after removal of epiphytes from the host branches with naturally high loads cannot equalize the leaf production values of branches with naturally low loads of epiphytes. Leaf production of branches with naturally low loads of epiphytes was distinctly higher than in the treatments with *Tillandsia* removal. This is an interesting result because the highest value of new leaf production was found in branches with natural low epiphyte loads, indicating a "secondary interference", additional to the physical presence of the epiphytes (i.e., structural parasites). This "remaining" secondary interference is highlighted by the lower leaf production upon the removal treatment in comparison with leaf production in trees resp. branches having naturally low epiphyte loads. This secondary interference may be linked to chemical compounds or microorganisms that can be maintained in those branches after *Tillandsia* removal, inhibiting leaf sprouting for a longer period. The observed increase in the number of new leaves after three years from the removals also supports this conclusion. In average, leaf production for branches after three years of epiphyte removal was 50% less than that observed in those branches with naturally low loads. This pattern suggests that the "secondary interference" acts for a longer time after the "primary physical interference" has disappeared. In addition, the growth of *Tillandsia recurvata* on *Prosopis laevigata* branches determined notorious changes in the host wood, such as a different distribution of secondary xylem cells and a reduction in the number and diameter of vessels (Aguilar-Rodríguez et al., 2007). Such anatomical changes that would be affecting leaf production and wood recovering after *Tillandsia* removal may require several years to be reversed. New experiments are needed to analyze whether *Tillandsia* species can produce chemical or morphological constraints that negatively affect the production of new leaves in *Prosopis* branches with originally high load of epiphytes, even if these latter became removed.

Implications for conservation

Previous studies have suggested that some herbicides can be used to control *Tillandsia* epiphytes without causing phytotoxicity

to the host plant, due to differences in the absorption systems of the epiphytes and their hosts (Bartoli et al., 1993). Nevertheless, negative impacts on the host trees can be possible as a result of management practices such as branch pruning, application of chemicals, bark washing or brushing, etc., in order to remove epiphytes (Astegiano et al., 2007).

Quite obviously, management practices involving epiphyte removal that are not selective can affect negatively the diversity of *Tillandsia* and other epiphyte species with low regional abundances (Astegiano et al., 2007). Such consequences of management practices must be previously evaluated since the epiphytes are an important component of the ecosystem, representing an important percentage of total biomass in the forest canopy (Nadkarni et al., 2004). Epiphytes can accumulate considerable amounts of organic matter in the tree crowns, promoting the nutrient cycling, and they greatly contribute to maintain the biodiversity of forest communities (Díaz et al., 2010). Therefore, any practice that may negatively affect the diversity of epiphytes in the host trees may also threaten the biodiversity of the entire plant community.

Conclusion

Present study is an experimental approach to evaluate the possible effects of the presence of different epiphytes loads on the production of new leaves in *Prosopis alba* trees, considering also the position of the epiphytes within the tree crown zone of the hosts and the level of human disturbance of the investigated sites. We found significant differences in leaf production when comparing the experimental treatments with different epiphyte loads. On the other hand, the leaf production observed was generally higher in branches with naturally low load of epiphytes, compared with heavily epiphyte-infested branches, but also with branches wherefrom the epiphytes had been removed artificially. We also found a higher production of leaves in the bottom zone of the tree crown, compared with middle or upper zones. Regarding the effect of the removal of epiphytes, when comparing the short and medium response time (six months and three years after epiphyte extraction, respectively), we observed a significant higher production of leaves after three years. Finally we found no significant differences when comparing the leaf production of *Prosopis alba* at sites with different human disturbance intensities.

Acknowledgements

We thank local people for their collaboration in the logistics and for providing access to their properties during fieldwork, to Dr. Carlos Montaña for the useful suggestions on an early version of this manuscript and Julia Galetto by the professional English advice. We gratefully acknowledge two anonymous reviewers for the helpful comments during the reviewing process, which substantially improved the manuscript. Finally, we thank Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Secretaría de Ciencia y Técnica (SECyT) Universidad Nacional de Córdoba, Argentina, (Grant ID: 1495) for the financial support.

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