Original Paper

Ramet demography of *Aechmea distichantha* (Bromeliaceae) in two contrasting years in the understory and open areas of a South American xerophytic forest

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Abstract

The *Schinopsis balansae* forests of the Wet Chaco are characterized by convex areas with woody vegetation and plain areas with herbaceous vegetation. In the Wet Chaco, *Aechmea distichantha* is a terrestrial bromeliad that forms dense colonies in the understory and open areas of these forests. The aim of this study was to analyze the spatial and temporal variations in population dynamics of this bromeliad species. We monitored ramets growing in sun and shade conditions during two contrasting years. We analyzed the spatial and temporal variations in survival, flowering, and ramet production. Variations in survival, flowering, and ramet production were more marked between years than between habitats. During the year with wetter and milder temperature conditions, survival and ramet production were higher than during the drier year with more extreme temperatures. Survival of vegetative ramets was less variable than survival of young and reproductive ramets. In the colder year, lower winter temperatures reduced the populations in all stages, being more important in the open areas. Our results highlight the importance of low temperatures on *A. distichantha* demography at this xerophytic forest located at the southernmost distribution range of this bromeliad species.

Key words: bromeliads, Chaco, climate, demography, habitat.

Resumen

Los bosques de *Schinopsis balansae* del Chaco Húmedo presentan áreas convexas con leñosas y áreas planas con herbáceas. La bromeliácea terrestre *Aechmea distichantha* forma densas colonias en el sotobosque y en los bordes de áreas abiertas. Para analizar las variaciones espaciales y temporales de la dinámica poblacional de esta especie, monitoreamos ramets creciendo al sol y a la sombra durante dos años contrastantes. Analizamos las variaciones espaciales y temporales en la supervivencia, floración y producción de hijuelos. Las variaciones en supervivencia, floración y producción de hijuelos fueron más marcadas entre años que entre hábitats. La supervivencia de ramets fue mayor durante el año más lluvioso que durante el año más seco y de temperaturas más extremas. La supervivencia de los ramets vegetativos fue menos variable que la de los ramets jóvenes y reproductivos. En el año más frío, las bajas temperaturas invernales redujeron la población en todas las clases, siendo el efecto más importante en áreas abiertas. Los inviernos afectan marcadamente la demografía de *A. distichantha* en este bosque xerófitico ubicado en la porción más austral de su rango de distribución.

Palabras clave: bromelias, Chaco, clima, demografía, hábitat.
Introduction

Habitat heterogeneity has long been recognized as one of the main factors affecting plant distribution in many terrestrial ecosystems (Scheiner & Willig 2011). In forests and woodlands, this heterogeneity is increased due to variations in canopy structure and woody species composition (Thomsen et al. 2005; Barbier et al. 2008; Burton et al. 2011; Barberis et al. 2014), which may produce large differences in resource availability (e.g., light, nutrients, water) and environmental conditions (e.g., temperature) (Clark et al. 1996; Denslow et al. 1998; Ostertag 1998; Montgomery & Chazdon 2001). Even though there is a continuous gradient in resource availability and environmental conditions (Cogliatti-Carvalho et al. 1998, 2001), the environmental differences between contrasting shaded and open areas, like understory and treefall gaps, may affect plant growth and survival, and therefore plant population dynamics (Barberis & Tanner 2005; Fortini et al. 2010; Kuptz et al. 2010; Dalling et al. 2012; Myster 2012).

A conspicuous feature of several tropical and subtropical forests in America is the presence of dense populations of bromeliad species in their understories (Benzing 2000; Ticktin & Nantel 2004; Barberis & Lewis 2005; Brancalion et al. 2009; Rocha et al. 2015), which may also colonize treefall gaps and forest edges (Scarano et al. 2002; Sampaio et al. 2004; Skillman et al. 2005; Cavallero et al. 2009). Several studies have analyzed the structure and dynamic of bromeliad populations growing in the understory (Garcia-Franco & Rico-Gray 1995; Nunes-Freitas & Rocha 2001; Villegas 2001; Sampaio et al. 2002, 2004; Ticktin & Nantel 2004; Ticktin 2005; Lenzi et al. 2006; Duarte et al. 2007; Mantuano & Martinelli 2007; Rogalski et al. 2007). However, only a few of these studies analyzed the effects of different habitats on bromeliad population structure and dynamic (Sampaio et al. 2004, 2005).

Variability in climatic conditions is also known to affect growth and survival of understory plants, and therefore their population dynamics (Scheiner & Willig 2011). Among the most important climatic factors limiting plant population growth are water availability (e.g., drought) (Silva et al. 2015) and low temperatures (e.g., frosts) (Bremer & Jongejans 2010). The effects of climate conditions on plant growth and survival could be reduced or increased due to habitat conditions (Poorter & Hayashida-Oliver 2000). For instance, bromeliad plants growing in open areas receive a higher amount of water than those in the understory, because there is no canopy interception (Cavallero et al. 2009), but they are probably exposed to higher risk of frost damage (Steens 2000).

The Wet Chaco is a large sedimentary plain located in northern Argentina, western Paraguay and a small portion in the southwest of Brazil, which is covered by xerophytic forests, savannas, and tall grasslands (Prado 1993). In its southernmost area, known as Cuña Boscosa Santafesina, the dominant vegetation are the Schinopsis balansae Engl. forests (Lewis 1991). In these open forests, woody species distribution is associated with local environmental microheterogeneity (Lewis et al. 1997; Barberis et al. 1998). Patches of closed forests (about 10–12 m tall) are located in convex areas, separated by stretches of savanna-type vegetation in plain areas (Barberis et al. 2002). The understory of these shaded patches has lower light intensity and temperatures and higher humidity than sunny patches from open areas or forest edges (Cavallero et al. 2009). Two terrestrial bromeliads (Aechmea distichantha Lem. and Bromelia serra Griseb.) dominate the understory and forest edges of these forests (Barberis & Lewis 2005; Barberis et al. 2014).

In these forests, Aechmea distichantha is frequently found on the ground in the understory and forest edges (Barberis et al. 2014) but may also occur as an epiphyte (Alvarez Arnesi et al. 2018). It may propagate both sexually and asexually, but the latter is the more common way of reproduction in these forests (Cavallero et al. 2009). This tank bromeliad shows high phenotypic plasticity, and thus plants growing in contrasting habitats (e.g., understory and forest edges) showed marked differences in their leaf anatomy, plant architecture, biomass allocation, and reproductive traits (Cavallero et al. 2009, 2011; Freire et al. 2018). Because of this high phenotypic plasticity and differences in habitat conditions (e.g., light, temperature, rainfall), understory plants had smaller water tanks but probably received higher litterfall than plants located in forest edges or open areas (Cavallero et al. 2009; Montero et al. 2010). These differences in resource availability could be enhanced due to marked differences in climatic conditions (i.e. rainfall and high and low extreme temperatures) between years in the study area (Prado 1993). Therefore, A. distichantha
plants growing in contrasting habitats are expected to show differences in plant growth and survival due to differences in resource availability and environmental conditions. However, it is not known what the effects of differences in habitats (i.e. shaded and sunny patches) and in annual climatic conditions are on the growth and survival of different growth stages of this tank bromeliad. Therefore, in this study, we analyzed the growth, reproduction and survival of ramets at different growth stages from a terrestrial bromeliad (*Aechmea distichantha*) growing under sun and shade conditions in two contrasting years in a xerophytic forest (Barberis *et al.* 2002, 2014), located in the Wet Chaco at the southernmost range of its distribution (Barberis *et al.* unpublished data).

**Material and Methods**

**Study site**

The study was carried out in a 64-ha forest of *Schinopsis balansae* (Fig. 1) located at Las Gamas, Santa Fe, Argentina (29°28’S, 60°28’W) at 58 m a.s.l. (Barberis *et al.* 2002). The climate is humid temperate to warm, with a mean annual temperature of about 20 °C, but frosts are common in winter (Barberis *et al.* 2005). Mean annual rainfall for the study site is about 1000 mm, with mean monthly precipitation above 100 mm between October and April, and a dry period with mean monthly precipitation below 50 mm between May and September. Soils are Ochraclalf and Natraclalf, with low hydraulic conductivity and high sodium content (Barberis *et al.* 2005). There are no rocks on the topsoil, but the microtopography and soil moisture condition the structure and floristic composition of this xerophytic forest (Lewis *et al.* 1997; Barberis *et al.* 1998). In areas with convex microtopography, there are higher tree and shrub densities (Barberis *et al.* 2002), where two terrestrial bromeliads (*B. serrra* and *A. distichantha*) form dense populations (Barberis & Lewis 2005; Barberis *et al.* 2014).

**Study species**

*Aechmea distichantha* occurs as a terrestrial or epiphytic plant in deciduous, semideciduous and evergreen forests from sea level to an altitude of 2,400 m in southern Brazil, Bolivia, Paraguay, Uruguay and northern Argentina (Smith & Downs 1979). Its pungent leaves (about 30–100 cm long) are arranged forming a tank where water, organic matter, and seeds accumulate (Cavallero *et al.* 2009; Cogliatti-Carvalho *et al.* 2010; Barberis *et al.* 2011), allowing a diverse macrofauna of aquatic organisms (Torales *et al.* 1972; Montero *et al.* 2010). Like other tank bromeliads, it has absorptive foliar trichomes that have the capacity to take up water and nutrients from the tank (Leroy *et al.* 2016). It reproduces both sexually and asexually (Mercier & Guerreiro Filho 1990; Bernardello *et al.* 1991; Bianchi *et al.* 2000; Scrok & Varassin 2011; Freire *et al.* 2018). Ramets show high phenotypic plasticity; shade plants have longer leaves and thus are taller and have larger diameters, whereas sun plants have more leaves and larger sheath mass fraction and thus higher maximum tank water contents (Cavallero *et al.* 2009, 2011; Montero *et al.* 2010). Shade plants have heavier infructescences, longer rachis, more spikelets, a higher number of flowers/spikelet and a higher number of seeds/flower than those from sun plants (Freire *et al.* 2018). A specimen of this species was incorporated into the Juan Pablo Lewis Herbarium of the Universidad Nacional de Rosario (UNR 2303, Lewis 877).
Sampling procedure
In May 2006, we marked 360 ramets growing in shaded patches and 312 ramets growing in full sun. For each ramet, we measured its height from the top leaf to the soil, recorded whether it was flowering or not, and tagged it on its longer leaf. Based on the data of this first survey, as well as from our experience about the ecology of this bromeliad species, we recognized three life stages (i.e. flowering ramets, vegetative ramets, and young ramets) according to the presence of sexual reproductive structures and their height (sensu Sampaio et al. 2005) (Fig. 2). We used a height of 30 cm to separate vegetative from juvenile ramets because below this height the probability of flowering was nil.

In May 2007 and May 2008, for each tagged ramet we recorded its survival, measured its height, and recorded its reproductive state (i.e. flowering or not). We also recorded the production of new vegetative ramets. In 2007, we measured and tagged 88 new ramets in the shade and 86 in the sun, whereas in 2008, we measured 97 new ramets in the shade and 111 in the sun.

Climatic conditions during the study period
Annual rainfall was higher in 2006–2007 than in 2007–2008 (1,397 mm yr\(^{-1}\) vs. 847.5 mm yr\(^{-1}\)). Even though there were no differences in precipitations between both years in summer (Dec-Feb), higher precipitations were recorded in winter (Jun-Aug), spring (Sep-Nov) and fall (Mar-May) for the year 2006–2007 than for the year 2007–2008 (Estación Experimental Las Gamas, Ministerio de la Producción de la Provincia de Santa Fe, Fig. 3). Mean summer temperature was similar between 2006–2007 and 2007–2008. However, higher maximum absolute temperature (39.5 °C vs. 38.4 °C) and lower minimum absolute temperature (-5.6 °C vs. -2.1 °C) were recorded in 2007–2008 than in 2006–2007. Furthermore, in winter 2007–2008 the coldest temperatures from the last 40 years were recorded for the region under study (Instituto Nacional de Tecnología Agropecuaria, Estación Meteorológica Reconquista, <http://inta.gob.ar/documentos/estacion-meteorologica-reconquista>.

Data analyses
The effects of year, habitat and life stage on the probability of individual survival and on the probability of new ramet production were tested with generalized linear models (Binomial and Poisson distributions respectively, P < 0.05). The effects of year and habitat on the flowering probability of vegetative ramets were analyzed with generalized linear models (Binomial distribution, P < 0.05). To correct for overdispersion of the

Figure 2 – a-b. Aechmea distichantha plants growing in forest edges – a. vegetative ramet; b. flowering ramet.

Figure 3 – Monthly precipitation through the study period (2006-2007 and 2007-2008).
data, the models were fitted by quasi-maximum likelihood (Zuur et al. 2009). We used the protocol for model selection presented by Zuur et al. (2009). When the third order interactions were significant we run the analyses separately for each developmental stage. All analyses were done using the glm procedure of the AED library from the R package (ver. 3.3.0) (R Development Core Team 2016).

Results

Ramet survival was higher in 2006–2007 than in 2007–2008 in both habitats for all stage classes (Fig. 4; Tab. 1). Ramet survival was slightly higher for younger, and lower for reproductive ramets (Fig. 4). There were no differences between habitats in plant survival for young and flowering ramets, although the latter showed a contrasting pattern in both years the interaction was not statistically significant (Fig. 4; Tab. 1). For vegetative ramets, plant survival was higher in the shade than in the sun, and this effect was higher in 2006–2007 than in 2007–2008 (Fig. 4; Tab. 1).

Ramet production was higher for reproductive ramets than for vegetative and young ramets (Fig. 5). There were marked differences between years in ramet production from vegetative and from young ramets, but they differed in their patterns (Fig. 5; Tab. 2). Ramet production from vegetative ramets was higher in 2006–2007 than in 2007–2008, whereas ramet production from young ramets was lower in 2006–2007 than in 2007–2008 (Fig. 5; Tab. 2). There were also differences in ramet production between habitats but differed between stage classes (Fig. 5; Tab. 2). Ramet production from fruiting ramets was higher in the sun than

Figure 4 – Probability of survival (+/- s.e.m.) of *Aechmea distichantha* growing in the sun and in the shade for the two study periods – a. for young; b. for vegetative; c. for flowering ramets.

Figure 5 – a-c. Ramet production per individual (+/- s.e.m.) of *Aechmea distichantha* growing in the sun and in the shade for the two study periods – a. for Young; b. for Vegetative; c. for Flowering ramets.
in the shade, whereas the opposite pattern was observed for ramet production from young ramets. Ramet production from vegetative ramets was higher but not significantly different in the sun than in the shade (Fig. 5; Tab. 2).

There was a strong effect of year and habitat on flowering probability (Fig. 6; Tab. 3). The proportion of vegetative ramets that flowered was higher in the shade than in the sun, and lower in 2006–2007 than in 2007–2008 (Fig. 6; Tab. 3).

### Table 1 – Logistic regression models to analyze plant survival in different years and habitats for each class of ramets (YR = young ramets; VR = vegetative ramets; FR = flowering ramets). Deviance values, degrees of freedom, F values and their associated probabilities are shown for each factor and their interactions. Bold values denote significant results (i.e. P < 0.05).

|                      | df | Deviance | Resid. df | Resid. dev | F    | Pr (> F) |
|----------------------|----|----------|-----------|------------|------|----------|
| Year (Y)             | 1  | 9.93     | 202       | 197.5      | 9.74 | 0.002    |
| VR Habitat (H)       | 1  | 0.05     | 201       | 197.5      | 0.04 | 0.831    |
| Y × H                | 1  | < 0.001  | 200       | 197.5      | < 0.001 | 0.999 |
| Year (Y)             | 1  | 121.35   | 1108      | 1134.7     | 120.91 | < 0.001 |
| VR Habitat (H)       | 1  | 17.32    | 1107      | 1117.3     | 17.26 | < 0.001 |
| Y × H                | 1  | 6.26     | 1106      | 1111.1     | 6.23  | 0.013    |
| Year (Y)             | 1  | 7.38     | 102       | 135.8      | 7.09  | 0.009    |
| FR Habitat (H)       | 1  | 0.05     | 101       | 135.8      | 0.05  | 0.821    |
| Y × H                | 1  | 3.82     | 100       | 132.0      | 3.68  | 0.058    |

### Table 2 – Poisson regression models to analyze ramet production in different years and habitats for each class of ramets (YR = young ramets; VR = vegetative ramets; FR = flowering ramets). Deviance values, degrees of freedom, F values and their associated probabilities are shown for each factor and their interactions. Classes: YR, young ramets; VR, vegetative ramets; FR, flowering ramets. Bold values denote significant results (i.e. P < 0.05).

|                      | df | Deviance | Resid. df | Resid. dev | F    | Pr (> F) |
|----------------------|----|----------|-----------|------------|------|----------|
| Year (Y)             | 1  | 8.57     | 204       | 46.48      | 10.13 | 0.002    |
| VR Habitat (H)       | 1  | 6.36     | 205       | 55.05      | 7.52  | 0.007    |
| Y × H                | 1  | < 0.001  | 203       | 46.48      | < 0.001 | 0.999 |
| Year (Y)             | 1  | 5.38     | 1038      | 694.64     | 5.40  | 0.020    |
| VR Habitat (H)       | 1  | 3.51     | 1039      | 700.02     | 3.53  | 0.061    |
| Y × H                | 1  | 0.09     | 1037      | 694.55     | 0.09  | 0.763    |
| Year (Y)             | 1  | 0.79     | 207       | 189.04     | 0.87  | 0.354    |
| FR Habitat (H)       | 1  | 4.85     | 208       | 189.82     | 5.33  | 0.022    |
| Y × H                | 1  | 0.64     | 206       | 188.40     | 0.70  | 0.404    |
The dynamic of *Aechmea distichantha* populations was more affected by the environmental conditions of a year than by the habitat where the ramets grow: survival and ramet production were higher in the wetter and mild-temperature year, whereas fruiting was higher in the drier year. Likewise, other studies on bromeliad population dynamics highlighted the importance of drought due to a lower amount of rainfall and seasonality of rainfalls. For instance, microclimatic conditions affected the structure and dynamic of subpopulations of *Neoregelia cruenta* (Graham) L.B. Smith populations growing in the Brazilian restingas, and rainfall seasonality had a significant effect on its growth rate (Mantuano & Martinelli 2007). Likewise, *Aechmea magdalenae* (André) André ex Baker plants had lower survival (75%) and higher clonal reproduction in the seasonal moist forest of Barro Colorado Island, Panama, than in wet forest of Chocó, Colombia (97%) (Villegas 2001). However, in the epiphytic bromeliad *Vriesea sanguinolenta* Cogn. & Marchal growing in Panamanian rainforest neither growth nor survival were significantly affected by annual variation in rainfall (Zotz 2004).

The main source of mortality for *Aechmea distichantha* in our forest was the very low winter temperatures. This species has been reported as tolerant to low temperatures and there are many reports for plants cultivated outside its distribution range that have survived strong frosts or even beneath a thick layer of snow (Ensign 1958; Van Hyning 1958; Fisher 1963, 1964; Holmer 1966; Charley 1968; Bidlingmayer 1980; Jenkins 1999). However, it should be taken into account that the year ‘2006–2007’ was one of the coldest in the last 40 years and that our study site is located at the southernmost range of the distribution of this species (Barberis *et al.* unpublished data), where frosts seem to be one of the main factors limiting its distribution southward.

Lower survival of vegetative ramets in open areas could be related to different factors. These plants depend on their phytotelmata; ramets growing in the sun allocated more biomass to the sheath and thus have a larger tank that allows them to retain more water than plants from the shade (Cavallero *et al.*. 2009). Therefore, plants growing in the sun seem to be limited by nutrients, whereas those growing in the understory seem to be limited by water (Montero *et al.*. 2010). Plants growing in open areas experience a higher stress due to high light intensity, mainly in summer (Cavallero *et al.*. 2009), but they are also exposed to stronger frosts in winter (Barberis IM, personal observation). Even though most reports about temperature effects on *Aechmea distichantha* were not based on experiments, it seems that higher survival is achieved when the tank is filled with water, and the plant is protected by branches (Fisher 1963; but see Fisher 1964; Jenkins 1999). Finally, it is possible that other factors like small-scale population characteristics (*e.g.*, below- and aboveground interactions with other plants) could also affect plant survival, as has been suggested for *Aechmea nudicaulis* Griseb. plants in the sandy soils of the restingas (Sampaio *et al.*. 2005)

**Table 3** – Binomial regression models to analyze sexual reproduction for vegetative ramets in different years and habitats. Deviance values, degrees of freedom, Chi-squared values and their associated probabilities are shown for each factor and their interactions. Bold values denote significant results (*i.e.*, $P < 0.05$).

| Factor                  | df | Deviance | Resid. df | Resid. dev. | $P(>|\text{Chi}|)$ |
|-------------------------|----|----------|-----------|-------------|-------------------|
| Year (Y)                | 1  | 21.82    | 1140      | 916.7       | <0.001            |
| Habitat (H)             | 1  | 5.14     | 1141      | 938.5       | 0.020             |
| Y $\times$ H            | 1  | 0.02     | 1139      | 916.7       | 0.900             |

**Figure 6** – Flowering probability (+/- s.e.m.) for vegetative ramets of *Aechmea distichantha* growing in the sun and in the shade for the two study periods.
The higher flowering of ramets in the shade is probably associated with milder conditions in the understory. A similar pattern has been recorded for *Aechmea distichantha* in another study of these forests (Freire *et al.* 2018). In contrast, *A. distichantha* ramets growing in open areas showed a higher production of ramets than those growing in the understory. A similar pattern in ramet production was reported for *Aechmea magdalenae* plants in Panamanian forests (Villegas 2001), and for *Neoregelia johannis* (Carriére) L.B. Smith plants in an Atlantic Rain forest (Cogliatti-Carvallo & Rocha 2001), whereas the abundance of *Canistropis microps* (E. Morren ex Mez) Leme plants was negatively associated with light intensity in the understory of an Atlantic Rain forest (Nunes-Freitas & Rocha 2007). However, it should be considered that in most neotropical forests there are vertical and horizontal gradients in light intensity (Nunes-Freitas & Rocha 2007), and thus light environment is not a discrete, but a continuous variable, which may affect bromeliad architecture, physiology, and therefore growth and survival (Cogliatti-Carvalho *et al.* 1998). Therefore, it is likely that there is a full gradient in ramet production rate from open areas in gaps to shaded areas in the understory.

Ramet production was higher for reproductive ramets and very low for young ones. In contrast, Sampaio *et al.* (2005) recorded higher ramet production for young ramets and very low for reproductive ones. It is possible that young ramets of *Aechmea distichantha* allocate resources to grow rather than to produce a new ramet.

The probability of ramet production from young ramets significantly varied between habitats and years. In contrast, the probability of ramet production from vegetative ramets was constant across habitats, whereas the probability of ramet from reproductive ramets was constant across years. Similar results were observed for these ramet categories for *Aechmea nudicaulis* in different habitats, microhabitats, and years at the restingas (Sampaio *et al.* 2005).

Even though there are many reproductive individuals of *Aechmea distichantha* at our study site, the maintenance and increase in population growth are mainly based on clonal growth, as has been described for other terrestrial bromeliad species (e.g., *Aechmea magdalenae, Aechmea nudicaulis, Bromelia pinguis* L) (Brokaw 1983; Garcia-Franco & Rico-Gray 1995; Villegas 2001; Sampaio *et al.* 2005).

Our previous studies showed that *Aechmea distichantha* plants exposed to different environmental conditions (i.e. understory vs sunny areas) showed marked differences in leaf anatomy, plant architecture, biomass allocation, and reproductive traits (Cavallero *et al.* 2009, 2011; Freire *et al.* 2018). Despite these differences between habitats, the present study showed that the dynamic of *A. distichantha* populations was more affected by the environmental conditions of a particular year than by habitat conditions. These results highlight the importance of low temperatures on *A. distichantha* demography at this xerophytic forest located at the southernmost distribution range of this bromeliad species.

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### References

Alvarez Arnesi E, Barberis IM & Vesprini JL (2018) Distribución de epífitas vasculares sobre cuatro especies arbóreas en un bosque xerófítico del Chaco Húmedo, Argentina. Ecología Austral 28: 480-495.

Barberis IM & Lewis JP (2005) Heterogeneity of terrestrial bromeliad colonies and regeneration of *Acacia praecox* (Fabaceae) in a humid-subtropical-Chaco forest, Argentina. Revista de Biología Tropical 53: 377-385.

Barberis IM & Tanner EVJ (2005) Gaps and root trenching increase tree seedling growth in Panamanian semi-evergreen forest. Ecology 86: 667-674.

Barberis IM, Batista WB, Pire EF, Lewis JP & León RJC (2002) Woody population distribution and environmental heterogeneity in a Chaco forest, Argentina. Journal of Vegetation Science 13: 607-614.

Barberis IM, Boccanelli SI & Alzugaray C (2011) Terrestrial bromeliads as seed accumulation microsites in a xerophytic forest of Southern Chaco, Argentina. Bosque 32: 57-63.

Barberis IM, Lewis JP & Batista WB (2005) Heterogeneidad estructural de los bosques de la Cuña Boscosa de Santa Fe en distintas escalas espaciales. In: Oesterheld M, Aguiar MR, Ghera CM & Paruelo JM (eds.) La heterogeneidad de la...
vegetación de los agroecosistemas: un homenaje a Rolando J.C. León. Facultad de Agronomía, Universidad de Buenos Aires, Buenos Aires. Pp. 43-58.

Barberis IM, Pire EF & Lewis JP (1998) Spatial heterogeneity and woody species distribution in a Schinopsis balansae (Anacardiaceae) forest of the Southern Chaco, Argentina. Revista de Biología Tropical 46: 515-524.

Barberis IM, Torres PS, Batista WB, Magra G, Galetti L & Lewis JP (2014) Two bromeliad species with contrasting functional traits partition the understory space in a South American xerophytic forest: correlative evidence of environmental control and limited dispersal. Plant Ecology 215: 143-153.

Barbier S, Gosselin F & Balandier P (2008) Influence of tree species on understory vegetation diversity and mechanisms involved - A critical review for temperate and boreal forests. Forest Ecology and Management 254: 1-15.

Benzing DH (2000) Bromeliaceae. Profile of an Adaptive Radiation. Cambridge University Press, Cambridge. 708p.

Bernardello LM, Galetto L & Juliani HR (1991) Floral nectar, nectary structure and pollinators in some argentinean Bromeliaceae. Annals of Botany 67: 401-411.

Bianchi MB, Gibbs PE, Prado DE & Vesprini JL (2000) Studies on the breeding systems of understorey species of a Chaco woodland in NE Argentina. Flora 195: 339-348.

Bidlingmayer M (1980) Bromeliads in a Vero Beach garden. Journal of the Bromeliad Society 30: 74-75.

Brancalion PHS, Gabriel VA & Gómez JM (2009) Do terrestrial tank bromeliads in Brazil create safe sites for palm establishment or act as natural traps for its dispersed seeds? Biotropica 41: 3-6.

Bremer P & Jongejans E (2010) Frost and forest stand effects on the population dynamics of Asplenium socolpendrium. Population Ecology 52: 211-222.

Brokaw NVL (1983) Groundlayer dominance and apparent inhibition of tree regeneration by Aechmea magdalenae (Bromeliaceae) in a tropical forest. Tropical Ecology 24: 194-200.

Burton JL, Mladenoff DJ, Clayton MK & Forrester JA (2011) The roles of environmental filtering and colonization in the fine-scale spatial patterning of ground-layer plant communities in north temperate deciduous forests. Journal of Ecology 99: 764-776.

Cavallero L, Galetti L, López D, McCargo J & Barberis IM (2011) Morphological variation of the leaves of Aechmea distichantha Lem. plants from contrasting habitats of a Chaco forest: a trade-off between leaf area and mechanical support. Revista Brasileira de Biociências 9: 455-464.

Cavallero L, López D & Barberis IM (2009) Morphological variation of Aechmea distichantha (Bromeliaceae) in a Chaco forest: habitat and size-related effects. Plant Biology 11: 379-391.

Charley WB (1968) More and more outside. The Bromeliad Society Bulletin 18: 90.

Clark DB, Clark DA, Rich PM, Weiss S & Oberbauer SF (1996) Landscape-scale evaluation of understory light and canopy structure: methods and application in a neotropical lowland rain forest. Canadian Journal of Forest Research 26: 747-757.

Cogliatti-Carvalhalo L, Almeida DR & Rocha CFD (1998) Phenotypic response of Neoregelia johannis (Bromeliaceae) dependent on light intensity reaching the plant microhabitat. Selbyana 19: 240-244.

Cogliatti-Carvalhalo L & Rocha CFD (2001) Spatial distribution and preferential substrate of Neoregelia johannis (Carrière) LB Smith (Bromeliaceae) in a disturbed area of Atlantic Rainforest at Ilha Grande, RJ, Brazil. Revista Brasileira de Botanica 24: 389-394.

Cogliatti-Carvalhalo L, Freitas AFN, Rocha CFD & van Sluys M (2001) Variação na estrutura e na composição de Bromeliaceae em cinco zonas de restinga no Parque Nacional da Restinga de Jurubatiba, Macaé, RJ. Revista Brasileira de Botânica 24: 1-9.

Cogliatti-Carvalhalo L, Rocha-Pessoa TC, Nunes-Freitas AF & Rocha CFD (2010) Volume de água armazenado no tanque de bromélias, em restings da costa brasileira. Acta Botanica Brasileira 24: 84-95.

Dalling JW, Schnitzer SA, Baldeck C, Harms KE, John R, Mangan SA, Lobo E, Yavitt JB & Hubbell SP (2012) Resource-based habitat associations in a neotropical liana community. Journal of Ecology 100: 1174-1182.

Denslow JS, Ellison AM & Sanford RE (1998) Treefall gap size effects on above-and below-ground processes in a tropical wet forest. Journal of Ecology 86: 597-609.

Duarte AS, Vieira da Silva C, Puchalski A, Mantovani M, Silva JS & Reis MS (2007) Estrutura demográfica e produção de frutos de Bromelia antiacantha Bertol. Revista Brasileira de Plantas Medicinas, Botucatu 9: 3.

Ensignment EW (1958) Bromeliads in the Central Florida freeze. The Bromeliad Society Bulletin 8: 7.

Fisher WB (1963) Hardy bromeliad checklist. The Bromeliad Society Bulletin 13: 142.

Fisher WB (1964) An equivocal experiment. The Bromeliad Society Bulletin 14: 98.

Fortini L, Bruna E, Zarin D, Vasconcelos S & Miranda I (2010) Altered resource availability and the population dynamics of tree species in Amazonian secondary forests. Oecologia 162: 923-934.

Freire RM, Barberis IM & Vesprini JL (2018) Reproductive traits, floral visitors and seed production of Aechmea distichantha Lem. plants growing in different habitats of a South American xerophytic forest. Rodriguésia 69: 385-396.
García-Franco JG & Rico-Gray V (1995) Population structure and clonal growth in *Bromelia pinguin* L. (Bromeliaceae) in dry forests of coastal Veracruz, Mexico. Tulane Studies in Zoology and Botany 30: 27-37.

Holmer JO (1966) The cold tolerances of some bromeliads. The Bromeliad Society Bulletin 16: 60.

Jenkins DW (1999) Cold hardiness and cold sensitivity of bromeliads. Journal of the Bromeliad Society 49: 32-41.

Kuptz D, Grams T & Günter S (2010) Light acclimation of four native tree species in felling gaps within a tropical mountain rainforest. Trees 24: 117-127.

Lenzi M, Matos JZ & Orth AI (2006) Variação morfológica e reprodutiva de *Aechmea lindenii* (E. Morren) Baker var. *lindenii* (Bromeliaceae). Acta Botanica Brasilica 20: 487-500.

Leroy C, Carrias JF, Céréghino R & Corbara B (2016) The contribution of microorganisms and metazoans to mineral nutrition in bromeliads. Journal of Plant Ecology 9: 241-255.

Lewis JP (1991) Three levels of floristical variation in the forests of Chaco. Journal of Vegetation Science 2: 125-130.

Lewis JP, Pire EF & Barberis IM (1997) Structure, physiognomy and floristic composition of a *Schinopsis balansae* (Anacardiaceae) forest in the Southern Chaco, Argentina. Revista de Biología Tropical 45: 1013-1020c.

Mantuano DG & Martineili G (2007) Estrutura populacional e crescimento da bromélia clonal *Neoregelia cruenta* na restinga de Jurubatiba. Revista Brasileira de Biociências 5: 876-878.

Mercier H & Guerreiro Filho O (1990) Propagação sexuada de algumas bromélias nativas da mata atlântica: efeito da luz e da temperatura na germinação. Hoehnea 17: 19-26.

Montero G, Feruglio C & Barberis IM (2010) The phytotelmata and foliage macrofauna assemblages of a bromeliad species in different habitats and seasons. Insect Conservation and Diversity 3: 92-102.

Montgomery RA & Chazdon RL (2001) Forest structure, canopy architecture, and light transmittance in tropical wet forests. Ecology 82: 2707-2718.

Myster RW (2012) Spatial and temporal heterogeneity of light and soil water along a terra firme transect in Amazonian Ecuador: effects on tree seedling survivorship, growth, and allocation. Canadian Journal of Forest Research 42: 203-206.

Nunes-Freitas A & Rocha C (2007) Spatial distribution by *Canistropsis microps* (E. Morren ex Mez) Leme (Bromeliaceae: Bromelioideae) in the Atlantic rain forest in Ilha Grande, Southeastern Brazil. Brazilian Journal of Biology 67: 467-474.

Ostertag R (1998) Belowground effects of canopy gaps in a tropical wet forest. Ecology 79: 1294-1304.

Poorter L & Hayashida-Oliver Y (2000) Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest. Journal of Tropical Ecology 16: 481-498.

Prado DE (1993) What is the Gran Chaco vegetation in South America? I. A review. Contribution to the study of the flora and vegetation of the Chaco. V.” Candollea 48: 145-172.

R Development Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Disponível em <http://www.R-project.org> Access on 25 January 2018.

Rocha FS, Duarte LD & Waechter JL (2015) Positive association between *Bromelia balansae* (Bromeliaceae) and tree seedlings on rocky outcrops of Atlantic forest. Journal of Tropical Ecology 31: 195-198.

Rogalski JM, Reis A, Reis MS & Neto CD (2007) Estrutura demográfica da broméia clonal *Dyckia brevifolia* Baker, Rio Itajaí-Açu, SC. Revista Brasileira de Biociências 5: 264-266.

Sampaio MC, Araújo TF, Scarano FR & Stuefer JF (2004) Directional growth of a clonal bromeliad species in response to spatial habitat heterogeneity. Evolutionary Ecology 18: 429-442.

Sampaio MC, Perissé LE, Oliveira GA & Rios RI (2002) The contrasting clonal architecture of two bromeliads from sandy coastal plains in Brazil. Flora 197: 443-451.

Sampaio MC, Picó FX & Scarano FR (2005) Ramet demography of a nurse bromeliad in a Brazilian restingas. American Journal of Botany 92: 674-681.

Scarano FR, Duarte HM, Rôças G, Barreto SMB, Amado EF, Reinert F, Wendt T, Mantovani A, Lima HRP & Barros CF (2002) Acclimation or stress symptom? An integrated study of intraspecific variation in the clonal plant *Aechmea bromeliifolia*, a widespread CAM tank-bromeliad. Botanical Journal of the Linnean Society 140: 391-401.

Scheiner SM & Willig MR (2011) The theory of Ecology. University of Chicago Press, Chicago. 408p.

Schor GJ & Varassin IG (2011) Reproductive biology and pollination of *Aechmea distichantha* Lem. (Bromeliaceae). Acta Botanica Brasilica 25: 571-576.

Silva KA, Andrade JR, Santos JMFF, Lopes CGR, Ferraz EMN, Albuquerque UP, Lima Araújo E (2015) Effect of temporal variation in precipitation on the demography of four herbaceous populations in a tropical dry forest area in Northeastern Brazil. Revista de Biología Tropical 63: 903-914.

Skillman JB, Garcia M, Virgo A & Winter K (2005) Growth irradiance effects on photosynthesis and growth in two co-occurring shade tolerant neotropical perennials of contrasting photosynthetic pathways. American Journal of Botany 92: 1811-1819.

Rodriguésia 71: e00262018. 2020
Smith LB & Downs RJ (1979) Bromeliaceae, subfamily Bromeliioideae. Flora Neotropica Monograph 14: 1493-2142.

Steens A (2000) Cold sensitivity in bromeliads. Journal of the Bromeliad Society 50: 153-154.

Thomsen RP, Svenning J-C & Balslev H (2005) Overstorey control of understorey species composition in a near-natural temperate broadleaved forest in Denmark. Plant Ecology 181: 113-126.

Ticktin T & Nantel P (2004) Dynamics of harvested populations of the tropical understorey herb *Aechmea magdalenae* in old-growth versus secondary forests. Biological Conservation 120: 461-470.

Ticktin T (2005) Applying a metapopulation framework to the management and conservation of a non-timber forest species. Forest Ecology and Management 206: 249-261.

Torales GJ, Hack WH & Turn B (1972) Criaderos de Culicidos en bromeliáceas del NW de Corrientes. Acta Zoológica Lilloana 29: 293-308.

van Hyning O (1958) What the freeze did to my bromeliads. The Bromeliad Society Bulletin 8: 8.

Villegas AC (2001) Spatial and temporal variability in clonal reproduction of *Aechmea magdalenae*, a tropical understorey herb. Biotropica 33: 48-59.

Zotz G (2004) Growth and survival of the early stages of the heteroblastic bromeliad, *Vriesea sanguinolenta*. Ecotropica 10: 51-57.

Zuur AF, Ieno EN, Walker N, Saveliev AA & Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York. 574p.