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Original Paper

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

Ignacio Martín Barberis[1,2,3,4], *Graciela Klekailo*[1], *Juliana Albertengo*[1], *Juan Ignacio Cárcamo*[1], *José María Cárcamo*[1] & *Luciano Galetti*[1]

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 en 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 xerofítico ubicado en la porción más austral de su rango de distribución.

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

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[1] Universidad Nacional de Rosario, Facultad de Ciencias Agrarias, Campo Experimental Villarino, C.C. 14, S2125ZAA, Zavalla, Argentina.

[2] Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de Rosario, Inst. Investigaciones en Ciencias Agrarias de Rosario, S2125ZAA, Zavalla, Argentina.

[3] ORCID: <https://orcid.org/0000-0002-6605-9270>

[4] Author for correspondence: ignaciobarberis@yahoo.com

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 (García-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 ramets 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 (29º28'S, 60º28'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 ºC, 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 Ochracualf and Natracualf, 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. serra* and *A. distichantha*) form dense populations (Barberis & Lewis 2005; Barberis *et al*. 2014).

Figure 1 – a-b. Different habitats of the *Schinopsis balansae* forest – a. forest edge; b. understory in convex areas.

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.

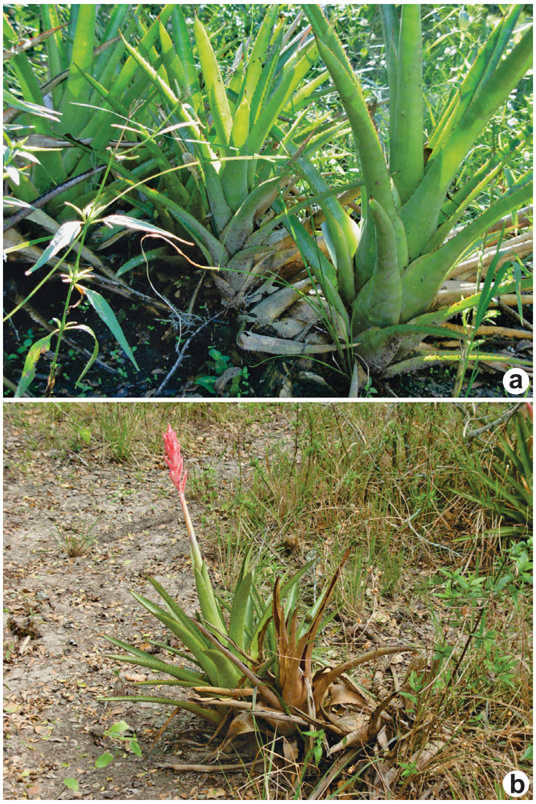

Figure 2 – a-b. *Aechmea distichantha* plants growing in forest edges – a. vegetative ramet; b. flowering ramet.

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 ºC *vs.* 38.4 ºC) and lower minimum absolute temperature (-5.6 ºC *vs.* -2.1 ºC) 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

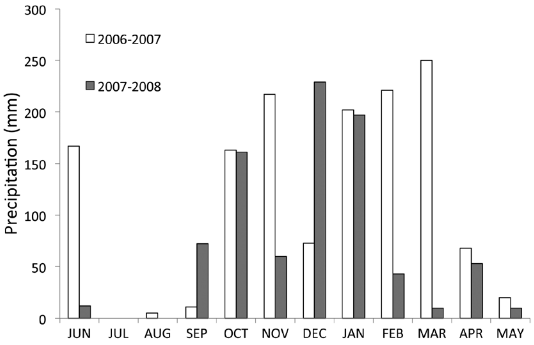

Figure 3 – Monthly precipitation through the study period (2006-2007 and 2007-2008).

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

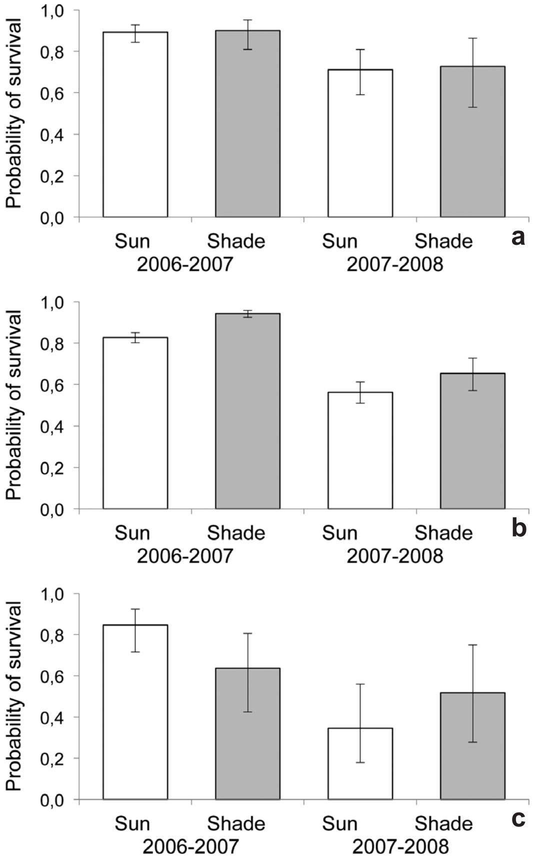

Figure 4 – Probability of survival (+/- s.e.m.) of *Aechmea distichantha* growing in the sun and in the shade for the two study periods – a. for young; b. for vegetative; c. for flowering ramets.

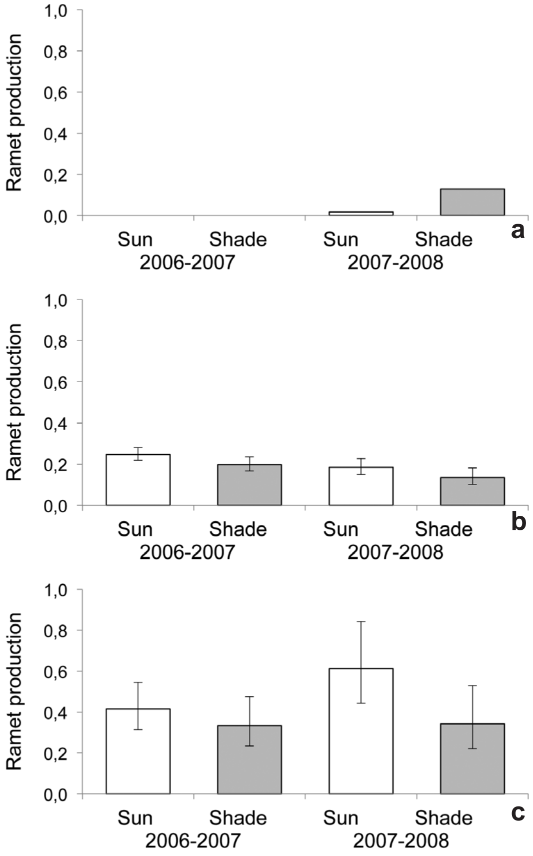

Figure 5 – a-c. Ramet production per individual (+/- s.e.m.) of *Aechmea distichantha* growing in the sun and in the shade for the two study periods – a. for Young; b. for Vegetative; c. for Flowering ramets.

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

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 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)
YR	Year (Y)	1	8.57	204	46.48	10.13	**0.002**
	Habitat (H)	1	6.36	205	55.05	7.52	**0.007**
	Y × H	1	< 0.001	203	46.48	< 0.001	0.999
VR	Year (Y)	1	5.38	1038	694.64	5.40	**0.020**
	Habitat (H)	1	3.51	1039	700.02	3.53	0.061
	Y × H	1	0.09	1037	694.55	0.09	0.763
FR	Year (Y)	1	0.79	207	189.04	0.87	0.354
	Habitat (H)	1	4.85	208	189.82	5.33	**0.022**
	Y × H	1	0.64	206	188.40	0.70	0.404

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.* $P < 0.05$).

	df	Deviance	Resid. df	Resid. dev.	P(> |Chi|)
Year (Y)	1	21.82	1140	916.7	**<0.001**
Habitat (H)	1	5.14	1141	938.5	**0.020**
Y × H	1	0.02	1139	916.7	0.900

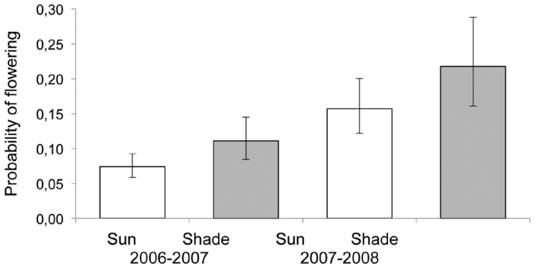

Figure 6 – Flowering probability (+/- s.e.m.) for vegetative ramets of *Aechmea distichantha* growing in the sun and in the shade for the two study periods.

Discussion

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).

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 *Canistropsis 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 pinguin* L) (Brokaw 1983; García-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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