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Phenotypic plasticity in *Bromelia serra* Griseb.: morphological variations due to plant size and habitats with contrasting light availability

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ABSTRACT: (Phenotypic plasticity in *Bromelia serra* Griseb.: morphological variations due to plant size and habitats with contrasting light availability). In the understory of the *Schinopsis balansae* Engl. forests of the Wet Chaco there are dense populations of *Bromelia serra*. The individuals of this strictly terrestrial bromeliad grow in the sun as well as in the shade of the understory. Studies carried out with a facultative epiphytic bromeliad, *Aechmea distichantha* Lem., which also lives in the understory of these forests and whose foliar bases form a tank (phytotelmata), showed the existence of differences in plant architecture and biomass allocation due to plant size (apparent phenotypic plasticity) and to environmental conditions (true phenotypic plasticity). Thus, to evaluate whether the architecture and biomass allocation of a strictly terrestrial bromeliad are also affected by habitat and by plant size, we selected 22 plants of *B. serra* from open areas and 22 from the understory. The selected plants covered the whole range of plant size. For each plant, we characterized its rosette (height, diameter and number of leaves) and measured the length and width of the longest leaf. The plants were split into stem and leaves (sheaths and blades), weighed, and then several biomass allocation indexes were derived. At a similar biomass, plants growing in the sun had shorter leaves, with a lower length: width ratio than those from the understory, but there were no differences between habitats with regard to plant height, diameter or different biomass fractions. These results suggest that *B. serra* (a strictly terrestrial bromeliad) shows a high apparent plasticity in most variables, but low true phenotypic plasticity in response to environmental differences.

Key words: bromeliads, Chaco, phenotypic plasticity, size-related variation, understory.

RESUMEN: (Plasticidad fenotípica en *Bromelia serra* Griseb.: variaciones morfológicas debidas al tamaño de la planta y al ambiente lumínico). En el sotobosque de los quebrachales de *Schinopsis balansae* Engl. del Chaco Húmedo crecen densas colonias de *Bromelia serra*. Los individuos de esta bromeliácea estrictamente terrestre se desarrollan tanto al sol como a la sombra del sotobosque. Estudios realizados con una bromeliácea epífita facultativa, *Aechmea distichantha* Lem., que también habita en el sotobosque de estos quebrachales y cuyas bases foliares forman un tanque (fitotelmata), verifican la existencia de diferencias en arquitectura y asignación de biomasa debido al tamaño de las plantas (plasticidad fenotípica aparente) y a las condiciones ambientales (plasticidad fenotípica real). Para evaluar si la arquitectura y asignación de biomasa de una bromeliácea estrictamente terrestre son afectadas por el hábitat y por el tamaño de las plantas, se seleccionaron 22 plantas de *B. serra* de áreas abiertas y 22 plantas del sotobosque que abarcaran todo el rango de variación de tamaño. Para cada planta se caracterizó su roseta (altura, diámetro y número de hojas) y se le midió el largo y ancho de la hoja más larga. Además, las plantas fueron separadas en tallo y hojas (vainas y láminas), pesadas, y se derivaron índices de asignación de biomasa. A igualdad de biomasa, las plantas que crecen al sol tienen hojas más cortas, con una menor relación largo:ancho que las del sotobosque. Sin embargo, no se observaron diferencias entre hábitats respecto a la altura, el diámetro, o la biomasa de distintas fracciones. Estos resultados sugieren que *B. serra* (bromeliácea estrictamente terrestre) muestra una elevada plasticidad aparente, pero una baja plasticidad fenotípica real en respuesta a diferencias ambientales.

Palabras-clave: bromeliáceas, Chaco, plasticidad fenotípica, sotobosque, variaciones en tamaño.

INTRODUCTION

The phenotypic traits of a plant may vary depending on environmental conditions, ontogeny, or both (McConaughay & Coleman 1999, Wright & McConaughay 2002, Weiner 2004). Plants growing under different environmental conditions may differentially allocate biomass to leaves, stem, or roots in order to optimize the capture of light, water, nutrients, and carbon dioxide, and therefore to maximize their plant growth rate (Bloom *et al.* 1985). The potential of an organism to produce a range of different phenotypes in response to environmental variations is known as 'true' phenotypic plasticity

(DeWitt & Willson 1998). One of the most widely studied environmental factors has been the response of plants to light quality and quantity (Hutchings & de Kroon 1994, Gratani 2014, Turcotte & Levine 2016).

During their growth and development, plants experience morphological, anatomical, and physiological changes related to their passage through different ontogenetic phases, such as vegetative growth, flowering, and fruiting (Zotz 2000, Schmidt *et al.* 2001, Zotz *et al.* 2001, Hietz & Wanek 2003, Petit *et al.* 2014). Since many of these allocation patterns follow allometric trajectories, allocation plasticity may also be the result of plant size, or

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'apparent plasticity' (McConaughay & Coleman 1999, Wright & McConaughay 2002, Weiner 2004, Chambel *et al.* 2005). Trait variation due to environmental factors (i.e. 'true plasticity') can be distinguished from 'apparent plasticity' by comparing plants of the same size growing in different habitats (Evans 1972).

In many xerophytic, semideciduous, and evergreen forests of the Neotropical region, dense populations of terrestrial bromeliads are frequently found in the understory, as well as in forest edges and open areas (Pfutsch & Smith 1988, Lee *et al.* 1989, Benzing 2000, Villegas 2001, Sampaio *et al.* 2002, Scarano *et al.* 2002, Freitas *et al.* 2003, Skillman *et al.* 2005, Mantuano & Martinelli 2007, González-Salvatierra *et al.* 2013, Barberis *et al.* 2014). The light environment where these species grow is usually very heterogeneous, from direct sunlight in open areas to the penumbra of the understory, as well as all the intermediate conditions in the light gradient (Lee *et al.* 1989, González-Salvatierra *et al.* 2013, Barberis *et al.* 2014). Plant phenotypic plasticity to light quality and quantity has been widely shown in epiphytic, facultative epiphytic, as well as in terrestrial bromeliads (Cogliatti-Carvalho *et al.* 1998, Scarano *et al.* 2002, Freitas *et al.* 2003, Lenzi *et al.* 2006, de Oliveira *et al.* 2008, Batagin *et al.* 2009, Voltolini & Santos 2011, Reinert *et al.* 2013, Rodrigues Pereira *et al.* 2013, Custódio *et al.* 2016, Ebel *et al.* 2016, North *et al.* 2016). In contrast, phenotypic variation due to plant size has been mainly analyzed in epiphytic or facultative epiphytic bromeliads (Schmidt & Zotz 2001, Zotz *et al.* 2002, Hietz & Wanek 2003, Zotz *et al.* 2004, Cavallero *et al.* 2009, Petit *et al.* 2014), and to our knowledge, there is no study that jointly analyzes the effects of habitats and plant size on plant morphology of strictly terrestrial bromeliads.

The 'quebrachales' of *Schinopsis balansae* Engl. (Anacardiaceae) from the southern Wet Chaco (Lewis 1991, Lewis *et al.* 1997) are open xerophytic forests, where the distribution of woody species is associated with environmental heterogeneity (Barberis *et al.* 2002). In convex areas, there are patches of closed forests about 10-12 m in height, that alternate with savanna type patches located in plain areas (Barberis *et al.* 2002). In the understory of these convex areas there are dense populations of two bromeliad species *Bromelia serra* Griseb. and *Aechmea distichantha* Lem. (Barberis & Lewis 2005, Barberis *et al.* 2014). Both species produce offspring by asexual reproduction (Smith & Downs 1979), and ramets from a same genet exposed to different environmental conditions show different phenotypes (i.e. modular plasticity *sensu* de Kroon *et al.* 2005). Therefore, there is a morphological gradient between modules completely exposed to full sunlight and those growing in the shade, with a set of intermediate phenotypes along the whole environmental gradient. Studies carried out with *A. distichantha*, a facultative epiphytic bromeliad that in these forests mainly grow on the ground and whose leaf bases form a tank where water and organic matter accumulate (i.e. phytotelmata), showed that the architecture and biomass

allocation of these plants depend both on environmental conditions (i.e. true phenotypic plasticity) and on plant size (i.e. apparent phenotypic plasticity) (Cavallero *et al.* 2009, Montero *et al.* 2010, Cavallero *et al.* 2011). Even though there is information about true phenotypic plasticity in strictly terrestrial bromeliads, to the best of our knowledge no study has evaluated their apparent phenotypic plasticity (i.e. plasticity associated with plant size). Therefore, the objective of this work was to explore variations in plant architecture and biomass allocation of a terrestrial bromeliad, *B. serra* along their whole size gradient and growing in sun or shade conditions (i.e. open areas or understory, respectively) in *S. balansae* forests of the southern Wet Chaco.

MATERIAL AND METHODS

Study site and analyzed species

The study was carried out at the Experimental Center 'Dr. Tito Livio Coppa', belonging to the Production Ministry of Santa Fe Province (Ministerio de la Producción de la provincia de Santa Fe), located at Las Gamas, department of Vera, Santa Fe province, Argentina (29° 28' S and 60° 28' W; 58 m a.s.l.). The mean annual rainfall is about 1000 mm, with a monthly average above 100 mm from October to April, and a dry season with precipitation below 100 mm between May and September (Barberis *et al.* 2005). Soils are Ochraqulf with a low hydraulic conductivity and high sodium content (Barberis *et al.* 2005). Soil moisture and microtopography condition the structure and floristic composition of this xerophytic forest (Lewis *et al.* 1997, Barberis *et al.* 1998). In convex areas, there are high densities of trees and shrubs (Barberis *et al.* 2002), and in their understory there are dense populations of two bromeliads, *B. serra* and *A. distichantha* (Barberis & Lewis 2005, Barberis *et al.* 2014). These 'quebrachales' are very heterogeneous and there is a strong variation in climatic conditions between the understory and the open areas (Cavallero *et al.* 2009). In the study area, canopy openness in the understory ranges from 18 to 25%, whereas in open areas it ranges from 35 to 72% (Barberis *et al.* unpublished data).

Several species of the genus *Bromelia* are frequently the dominant bromeliads growing in the understory of Neotropical forests (Medina *et al.* 1986, Lee *et al.* 1989, González-Salvatierra *et al.* 2013, Barberis *et al.* 2014, Rocha *et al.* 2015). This genus comprises 66 species with CAM photosynthetic mechanism (Fetene *et al.* 1990, Crayn *et al.* 2004) that mainly inhabit areas with savanna-type vegetation with dry and wet seasons located at low to middle altitudes (0 to 1200 m.a.s.l.) in Central and South America (Monteiro *et al.* 2015). *Bromelia serra* is a terrestrial bromeliad that grows in deciduous and semideciduous forests of southern Brazil, Bolivia, Paraguay and northern Argentina (Smith & Downs 1979). Its leaves are 30-100 cm long, with antrorse and retrorse spines located at their margins. It reproduces both, sexu-

ally and asexually (Smith & Downs 1979, Bianchi *et al.* 2000, Klekailo *et al.* 2012).

Plants of this terrestrial bromeliad grow in the sun, as well as in the shade, but show differences in the coloration of their leaves. Blades of plants growing in sunny areas are light green with reddish stripes, whereas those in the shade are dark green (Barberis, I.M.; *personal observation*). Similar observations have been reported for other *Bromelia* species, as well as for other species of the Bromelioideae subfamily (Medina *et al.* 1986, Lee *et al.* 1989, Cogliatti-Carvalho *et al.* 1998, González-Salvatierra *et al.* 2013, Custódio *et al.* 2016).

Sampling procedure

Twenty-two plants that covered the whole range of plant size were selected from each habitat (i.e. understory (range: 3.5-551.0 g) and open areas (range: 7.9-774.0 g)). The plants selected were at least three meters apart to ensure genetic independence between individuals. For each plant, the rosette was characterized (height, mean diameter, and number of leaves) and the length and width of the longest leaf were measured. Besides, plants were split into stem and leaves (blades and sheaths), and oven-dried at 60 °C for 120 hs. Due to technical problems during sampling, some variables could not be measured for a few plants (See degrees of freedom in the statistical analyses).

From the data of the different biomass components, the following allocation indexes were derived: stem mass fraction (SMF) = stem dry biomass / total dry biomass (g/g); sheath mass fraction (ShMF) = sheath dry biomass / total dry biomass (g/g); blade mass fraction (BMF) = blade dry biomass / total dry biomass (g/g); leaf:stem

ratio (L:S) = leaf dry biomass / stem dry biomass (g/g), and blade:sheath ratio (L:V) = blade dry biomass / sheath dry biomass (g/g). Finally, from data of the longest leaf the following variable was derived: length:width ratio (L:W) = length of the longest leaf / width of the longest leaf (cm/cm).

Statistical analyses

In order to distinguish true phenotypic plasticity from apparent phenotypic plasticity in plant architecture and biomass allocation in *B. serra* plants, general lineal models that considered the habitat (i.e. sun or shade) as a fixed factor and biomass as a covariate were used (Cavallero *et al.* 2009). Some variables were log10-transformed to meet with the assumptions of normality and variance homogeneity (Table 1). For all the variables analyzed, the slopes were similar for both habitats, therefore, the statistical tests were run again without including the interaction between biomass and the variable (Crawley 2013).

For each variable, a plasticity index was calculated to estimate its response to habitat. The estimated regression equations were used to obtain the mean values at each light environment (i.e. habitat) (App. 1). The phenotypic plasticity index was calculated as the difference between maximum and minimum mean values between both light environments divided by the maximum mean value (Valladares *et al.* 2005). The advantage of this phenotypic plasticity index, which varies between 0 and 1, is that it can be used to compare changes in variables expressed in different units and with a range of contrasting variation (Valladares *et al.* 2005, 2006). In order to analyze whether there were differences in the phenotypic plasticity index

Table 1. Results of the Covariance Analysis (ANCOVA) for variables related to plant architecture and biomass allocation for *Bromelia serra* individuals growing in the understory and in open areas of the *Schinopsis balansae* forest. The numerator and denominator degrees of freedom (d.f.), the F values, and their significance (P) are shown. Bold values denote significant effects corrected by Bonferroni (i.e. $P < 0.0033$). There was no Biomass \times Habitat interaction for any of the analyzed variables.

Variable (units)	Biomass			Habitat		
	d.f.	F	P	d.f.	F	P
Height (cm)	1,42	313.72	<0.0001	1,42	1.52	0.2243
Diameter (cm)	1,42	196.91	<0.0001	1,42	1.18	0.2844
Leaf number	1,41	106.56	<0.0001	1,41	0.02	0.9006
Stem biomass (g)	1,41	463.09	<0.0001	1,41	3.45	0.0705
Leaf biomass (g)	1,41	7.774.14	<0.0001	1,41	2.36	0.1324
Blade biomass (g)	1,42	2.584.77	<0.0001	1,42	1.10	0.2993
Sheath biomass (g)	1,41	752.32	<0.0001	1,41	2.79	0.1027
Leaf:Stem ratio (g g ⁻¹)	1,41	39.67	<0.0001	1,41	2.16	0.1491
Blade:Sheath ratio (g g ⁻¹)	1,41	19.11	<0.0001	1,41	2.48	0.1227
Stem mass fraction (g g ⁻¹)	1,42	73.50	<0.0001	1,42	0.53	0.4706
Blade mass fraction (g g ⁻¹)	1,42	52.84	<0.0001	1,42	0.96	0.3340
Sheath mass fraction (g g ⁻¹)	1,42	3.58	0.0653	1,42	0.27	0.6092
Leaf length (cm)	1,38	222.59	<0.0001	1,38	12.69	0.0010
Leaf width (cm)	1,38	47.53	<0.0001	1,38	0.38	0.5399
Length:Width ratio (cm cm ⁻¹)	1,38	90.74	<0.0001	1,38	14.34	0.0005

between different types of variables (i.e. architectural or biomass allocation) the Wilcoxon test for independent samples was used (Quinn & Keough 2002). These tests were carried out with the Rcmdr package in R (Fox & Bouchet-Valat 2016).

RESULTS

Larger plants were taller, had larger diameter, and larger biomass for all components (blades, sheaths, and stems), in addition to a higher number of longer and wider leaves (Table 1, Fig. 1). With regard to biomass

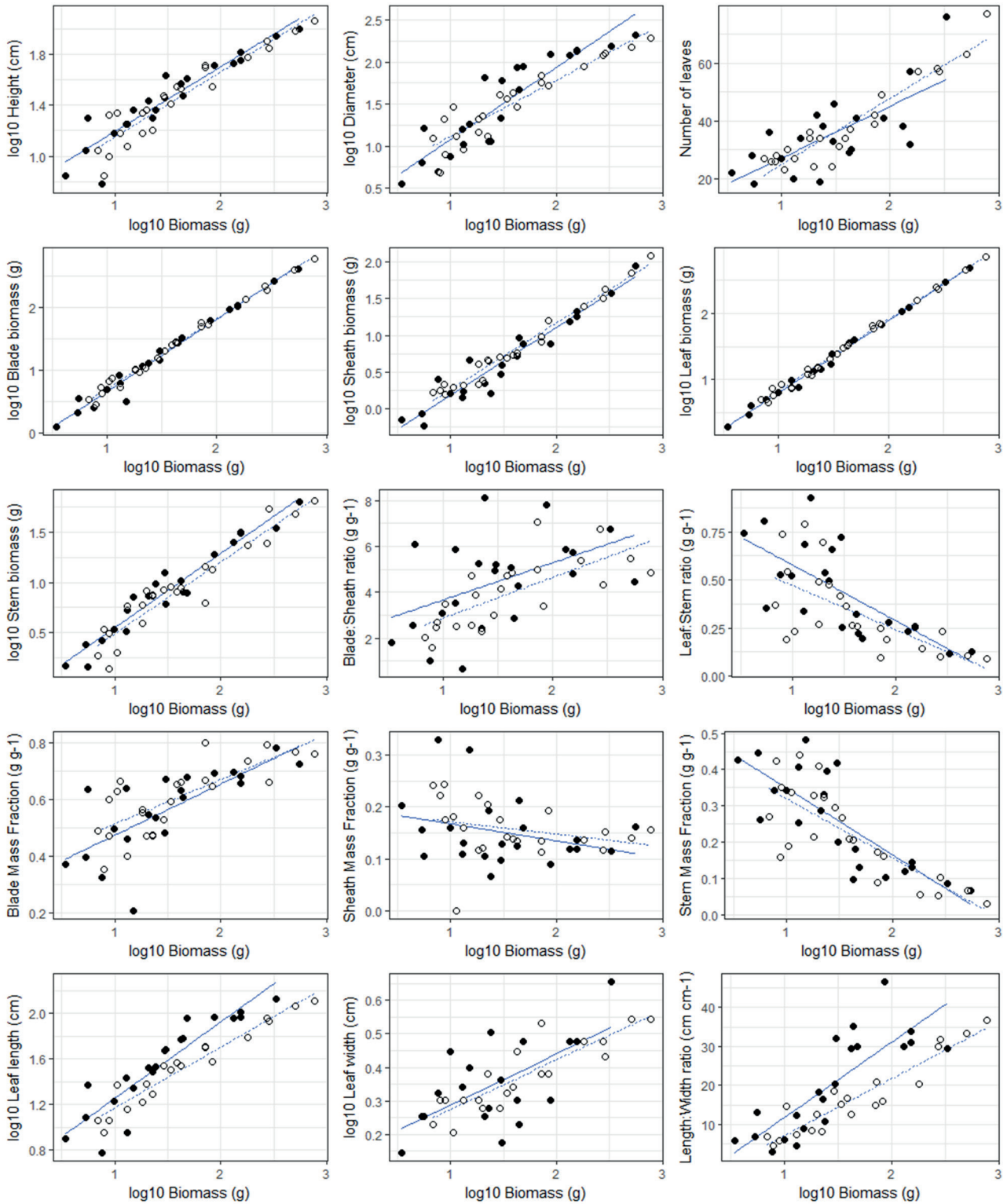


Figure 1. Variation in architectural and biomass allocation variables as a function of biomass for plants growing in the understory (filled circles) and in open areas (empty circles). Regression lines are shown for each group (understory, continuous line; open areas, discontinuous lines).

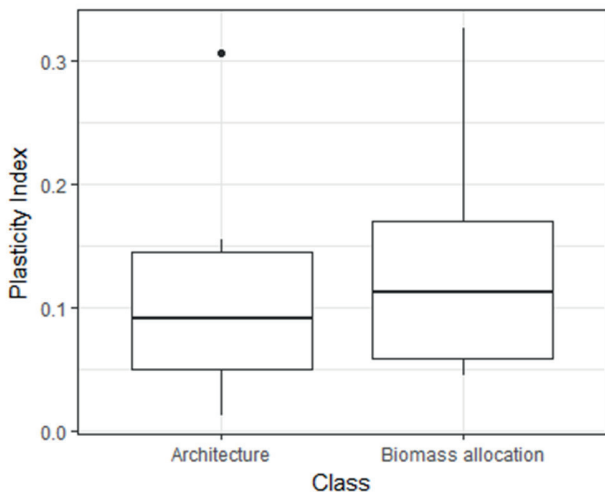


Figure 2. Boxplot of plasticity index for architectural and biomass allocation variables. Each boxplot includes the 25th percentile, the median, and the 75th percentile. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles.

allocation, an increase in biomass was associated with an increase in leaf mass fraction (LMF), a reduction in stem mass fraction (SMF) and a reduction in leaf:stem ratio, but there were no major changes in sheath mass fraction (ShMF), thus leading to an increase in blade:sheath ratio (Table 1, Fig. 1). At a similar biomass, plants growing in the shade had longer leaves, with a higher length-width ratio. However, there were no differences in height, diameter, leaf width, or biomass of the different fractions (Table 1, Fig. 1). The phenotypic plasticity indexes were very low for architectural variables, as well as for biomass allocation variables, and there were no differences between them ($W=20.0$; $P=0.4559$; Fig. 2).

DISCUSSION

In this study carried out with *B. serra*, a strictly terrestrial bromeliad, most of the variables analyzed showed an effect of plant size (i.e. apparent phenotypic plasticity), but there was no effect of habitat (i.e. true phenotypic plasticity), nor any interaction between both factors. These results contrast with those obtained for *A. distichantha*, a tank bromeliad that also grows in the understory of these xerophytic forests, which showed effects of both types of phenotypic plasticity for most of the variables analyzed (Cavallero *et al.* 2009, 2011). Therefore, of the two bromeliad species coexisting in the understory of the *S. balansae* forests, the strictly terrestrial bromeliad *B. serra* might be less plastic than the facultative epiphytic bromeliad *A. distichantha* in its response to environmental conditions regarding plant architecture and biomass allocation (Cavallero *et al.* 2009, 2011).

For *B. serra*, only two variables associated with leaf length and leaf form (length:width ratio) showed differences between habitats: plants in sunny locations had shorter leaves, and a lower length:width ratio than shaded plants. In both cases, morphological differences

between habitats remained constant through the whole range of plant size. Similar patterns in response to habitat variation have been reported for other bromeliad species (Cogliatti-Carvalho *et al.* 1998, Lenzi *et al.* 2006, Leroy *et al.* 2009, Cavallero *et al.* 2011, Custódio *et al.* 2016). These architectural changes in plants of *B. serra* growing in different habitats are likely to be associated with light capture (e.g. narrower and longer leaves in the shade), whereas the higher number of habitat-related phenotypic changes reported for *A. distichantha* have been shown to affect not only light capture but also water and nutrient dynamics (Cavallero *et al.* 2009, 2011). These differences could be attributed to the fact that the architectural and biomass allocation differences between tank bromeliads growing in sun and shade conditions also affect their ability to capture, retain, or lose water from their tanks (Cavallero *et al.* 2009, Petit *et al.* 2014). Moreover, as these plants grow there are also changes in their evaporating areas and projected leaf areas (Zotz & Thomas 1999, Cavallero *et al.* 2009). In some tank bromeliads, these phenotypic differences between habitats are translated into differences in their population dynamics (Sampaio *et al.* 2005, Barberis *et al.* unpublished data).

The lack of an environmental response for some architectural variables, such as height and diameter, could be associated with morphological characteristics of *Bromelia* species. *Bromelia balansae* plants modified their architecture during their blooming stage by folding back their leaves, which are normally displayed horizontally, parallel to the ground (Romero & Vasconcellos-Neto 2005). This architectural modification means that sometimes it is possible to find older plants that despite being larger are shorter than younger ones (Barberis, I.M.; *personal observation*). On the other hand, although plants in the sun had shorter leaves than plants in the shade, the lack of habitat effect on plant diameter could be attributed to ellipsoidal shapes developed by these plants due to growth limitations by other plants or by removal or destruction of some of their leaves (Barberis, I.M.; *personal observation*).

Some terrestrial bromeliads (e.g. *Ananas comosus* and *Ananas ananassoides*) growing in different environmental conditions (e.g. sun vs. shade), showed several physiological differences, but no differences in biomass allocation (Medina *et al.* 1991, 1993, 1994). Similarly, several studies with other species of *Bromelia*, which did not evaluate the plant architecture or biomass allocation, but reported differences in leaf coloration or in chlorophyll content, also found physiological differences between plants growing in different habitats (Medina *et al.* 1986, Lee *et al.* 1989, Fetene *et al.* 1990, Fetene & Lüttge 1991). These studies suggested that while there may not be a habitat effect on plant architecture or biomass allocation, these plants may differ in their functional response to environmental conditions.

Most studies analyzing the existence of phenotypic plasticity in bromeliads, evaluated contrasting habitats (e.g. sun vs. shade, or gap vs. understory); however,

plants in the wild are exposed to a continuous gradient of light intensity (Cogliatti-Carvalho *et al.* 1998). Moreover, within a plant there is a gradient of leaf light exposure conditions, from young leaves located in the center, and thus more exposed to sunlight, to the older ones located at the bottom and thus more shaded (Medina *et al.* 1994). Therefore, studies on bromeliad phenotypic plasticity should be conducted under controlled light environment, following plant growth and considering biomass allocation to different components (root, stem, sheath, and blades), as well as plant leaf area.

Finally, it has been suggested that phenotypic plasticity contributes to the ability of species to occupy broader ranges of environmental conditions and to better exploit resource-rich habitats (Richards *et al.* 2006; but see Dostál *et al.* 2017). In agreement with this statement, *A. distichantha* which showed higher phenotypic plasticity than *B. serra*, has a wider distribution range than the latter (Smith & Downs 1979).

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