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Original Paper

Demographic structure of clonal, endemic, and endangered rheophyte bromeliad *Dyckia ibiramensis*: asexual *vs* sexual reproduction

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Abstract

In southern Brazil some species of *Dyckia* genus occur as rheophytes. *Dyckia ibiramensis* is an endemic bromeliad that occurs in discrete patches of the rocky banks along Itajaí do Norte River, Santa Catarina state. Four populations along Itajaí do Norte River were studied. In each population, all rosettes were counted and the diameter of each rosette was measured. The spatial distribution of the rosettes was identified as an isolated rosette or a clump. The clumps were classified according to the number of rosettes. The total number of rosettes per population ranged from 295 to 1,412. Most rosettes occur in clumps (98.1%), and 41% have reproductive rosettes. The number of rosettes per clump ranged from two to 43 rosettes. The percentage of reproductive rosettes per population ranged from 7.8 to 26.7%. The correlation between the number of clumps or between the total number of rosettes and the area of occupation was significant and positive. Few seedlings and isolated rosettes, production of offshoots occurred on both immature, and reproductive rosettes, and clumps with few rosettes can indicate the clonal propagation predominate in *D. ibiramensis*. Therefore, the maintenance and monitoring of the populations are essential for its long-term *in situ* conservation.
Key words: conservation, disjunctive distribution, life stages, occupation area and riparian plant.

Resumo

No Sul do Brasil, algumas espécies do gênero *Dyckia* ocorrem como reófitas. *Dyckia ibiramensis* é uma bromélia endêmica que ocorre em manchas discretas, em bancos de rocha ao longo do Rio Itajaí do Norte, estado de Santa Catarina. Quatro populações ao longo do Rio Itajaí do Norte foram estudadas. Em cada população, todas as rosetas foram contadas e o diâmetro de cada roseta foi medido. A distribuição espacial das rosetas foi classificada como uma roseta isolada ou um grupo. Os grupos foram classificados de acordo com o número de rosetas. O número total de rosetas por população variou de 295 até 1.412. A maioria das rosetas ocorreu em grupos (98,1%), e 41% dos grupos tinham rosetas reprodutivas. O número de rosetas por grupo variou de duas a 43 rosetas. A porcentagem de rosetas reprodutivas por população variou de 7,8 a 26,7%. A correlação entre o número de grupos ou entre o número total de rosetas e a área de ocupação foi positiva e significativa. Poucas plântulas e rosetas isoladas, produção de brotos ocorrendo tanto em rosetas imaturas como reprodutivas, e grupos com poucas rosetas podem indicar o predomínio da propagação clonal em *D. ibiramensis*. Portanto, a manutenção e o monitoramento das populações são essenciais para sua conservação *in situ*, em longo prazo.
Palavras-chave: conservação, distribuição disjuntiva, estágios de vida, área de ocupação e planta ripária.

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Introduction

In Brazil, Bromeliaceae Juss. appears in a single biome and constitutes a center of diversity, being the third most important family (1,400 species and 50 genera, with 14% of endemism) in the Atlantic Rainforest (Martinelli *et al.* 2008; BFG 2018).

Habitat loss is the main threat to bromeliad species in Atlantic Forest because several bromeliad species are endemic in small tracts of forest and restricted to particular habitats (Siqueira Filho & Tabarelli 2006; Janke 2014). In ecological terms, bromeliads may be described as a group of (luminous, hydric and nutritional) stress-tolerant tropical herbs with an accentuated tendency to occupy rupestrian environments, as well as to epiphytism (Benzing 1980).

In Brazil, the genus *Dyckia* Schult. & Schult. f. presents 141 species, of these 128 endemics (Forzza *et al.* 2015). However, there are a large number of specimens that are indeterminate or have inaccurate identifications, requiring urgent review (BFG 2015). According to Klein (1979), some bromeliads of the genus *Dyckia* occur as rheophytes. The occurrence of rheophytes is linked to the presence of swift-running rivers (van Steenis 1981).

In Brazil, demographic studies with species belonging to the rheophyte biological group are practically inexistent *in situ*, the only exception being the one with *Dyckia brevifolia* Baker (Rogalski & Reis 2009). The bromeliad *Dyckia ibiramensis* Reitz is an endemic rheophyte of Hercílio or Itajaí do Norte River, Ibirama municipality, Santa Catarina State (Reitz 1983). It is adapted to the extreme conditions of floods and ebb tides of the river (Reitz 1983; Klein 1990). It was classified as critically endangered and, since then, it has remained on the Official List of the Endangered Species of the Brazilian Flora in danger of extinction (EN) (MMA 2014).

The endemic species *D. ibiramensis* occurs in populations distributed along four kilometers in discrete patches of the rocky banks and it has an area of 12,067m^2 distributed along the Itajaí do Norte River (Hmeljevski *et al.* 2011), Itajaí hydrographic basin, Ibirama, State of Santa Catarina, Brazil.

According to Klein (1990), the successive catastrophic floods in the Itajaí Valley (in the 1980s) had a great impact on the species. In 2004, an authorization was given to build a small hydroelectric facility (PCH Ibirama/Energy Brennand) in the region where the species is found. This proposal would result in the submersion of 2.6% of these species rosettes (Hmeljevski *et al.* 2011), but three populations were submersed. Moreover, the possible construction of yet another hydroelectric power plant in the Itajaí-Açu River Basin are both concerning imminent risks for *in situ* conservation of *D. ibiramensis*, primarily from the loss of its natural habitat. Thus, studies of *D. ibiramensis* populations will provide a scientific rationale for the development of viable strategies for its *in situ* conservation.

To pursue this goal in the present study, we asked (*i*) what is the total number of rosettes in each population, (*ii*) what is the number of reproductive rosettes in each population, (*iii*) what is the main form of occurrence of the rosettes (isolated or clumped), (*iv*) what is the number of rosettes per clump, (*v*) what correlation might exist between rosette size (diameter) and sexual reproduction, (*vi*) how many clumps had reproductive rosettes, and (*vii*) what correlation might exist between the occupied area and total number of rosettes or number of clumps. To answer these questions, we characterized the demographic structure of four natural populations of *D. ibiramensis* across the Itajaí do Norte River.

Materials and Methods

Study area

The Itajaí River Basin has 15,500 km^2, which corresponds to approximately 16% of the territory of the Santa Catarina State (Comitê do Itajaí 2005). By considering its natural characteristics, the Itajaí hydrographic basin may be divided into: Upper, Middle and Lower Itajaí Valley. The Itajaí do Norte or Hercílio River, is part of the Upper Itajaí Valley and one of the Itajaí-Açu River tributaries, which is the main river of the Itajaí hydrographic basin (Comitê do Itajaí 2005).

The regional climate, according to Köeppen classification, is subtropical *Cfa* type with an annual average temperature of 18.5ºC, annual rainfall between 1,300 and 1,500 mm, and constant rainfall in the summer (Collaço 2003).

Dyckia ibiramensis Reitz (Bromeliaceae) − The species is classified as rupicolous, heliophyte and rare endemic rheophyte from southern Brazil (Klein 1990). According Hmeljveski *et al.* (2011), in 2008, *D. ibiramensis* presented nine population with an aggregated distribution, on an area of occupation of 12,067 m^2, and all rosettes were counted (7,366 and 15.3% were fertile) and classified according to diameter: smaller than 15 cm (3,117 rosettes with 4 reproductive rosettes); between 15 and 30 cm (2,262 rosettes with 303 reproductive rosettes); and larger than 30 cm (1,987 rosettes with 810 reproductive rosettes). This study did not indicate seedling presence.

Seeds are dispersed by wind, gravity, and water (Downs 1974; Hmeljevski *et al.* 2011). The bromeliad *D. ibiramensis* presented an intermediate genetic diversity ($\hat{H}_E$ = 0.219; 0.094), a pronounced fixation index ($\hat{f}$ = 0.642; 0.474) and high genetic structure (G_{ST} = 0.674; 0.356) according Hmeljevski *et al.* (2011) and Reis (2019), respectively. Thus, after the construction of small hydroelectric plant of Ibirama and the occurrence of two large floods there was a considerable loss of rosettes and of the genetic diversity, lower fixation index and genetic structure in the populations of *D. ibiramensis* (Reis 2019).

Sampling

Vouchers of *D. ibiramensis* are deposited in the Barbosa Rodrigues Herbarium (HBR 57925, altitude 226m, latitude 27º02'23"S, and longitude 49º33'59.36 W; HBR 57926, altitude 207m, latitude 27º. 02'11.21"S and longitude 49º33'35.55"W)," Itajaí, Santa Catarina State. In 2018, seven natural patches with *D. ibiramensis* were registered along the Itajaí do Norte or Hercílio River (Fig. 1). This study was conducted in four of these patches which were referred as "populations". The other patches were not studied due to the difficulty of access (floods and currents). In each population, all rosettes were counted and the diameter of each rosette was measured. The data obtained for each population were distributed in diameter classes of rosettes (cm).

The spatial distribution of the rosettes was identified as an isolated rosette or a clump. The clumps were classified according to the number of rosettes, on the following classes: 1 = 2–10 rosettes; 2 = 11–20 rosettes; 3 = 21–30 rosettes; 4 = 31–40 rosettes; and 5 = 41–50 rosettes.

The correlation between the percentage of reproductive rosettes and the center of each diameter class was estimated for each population by using Pearson's correlation coefficient (*r*) with $\alpha = 0.05$, according Steel & Torrie (1980).

Regarding the developmental stage of rosettes, the following was considered: those that did not show signs or production of inflorescence and/or fruit formation were considered immature and those that showed signs or production of inflorescence and/or fruit formation were considered reproductive, according Rogalski *et al.* (2017); and plants with up to four centimeters without connection to other rosette were considered seedlings.

In order to evaluate clonal production, 30 rosettes were tagged. The number of clones presented by each rosette and whether the rosette was either immature or reproductive was also observed. The vegetative growth (clonal) of *D. ibiramensis* was classified according to Lovett Doust (1981).

Due to the geological diversity of the Itajaí-Açu River bank (DNPM 1986; Curcio *et al.* 2006), the lithotype of the studied occurrence sites was identified by specialists.

Results

All the populations of *D. ibiramensis* are located on gneisses of the Santa Catarina Granulite Complex (Fig. 2). The bromeliad *D. ibiramensis* is a policarpic species or it presents iteroparity (i.e. the same rosette flowers repeatedly) with clonal propagation (basal and axillary).

The total number of rosettes per studied population ranged from 295 (Population III) to 1,412 (Population IV). In the evaluated

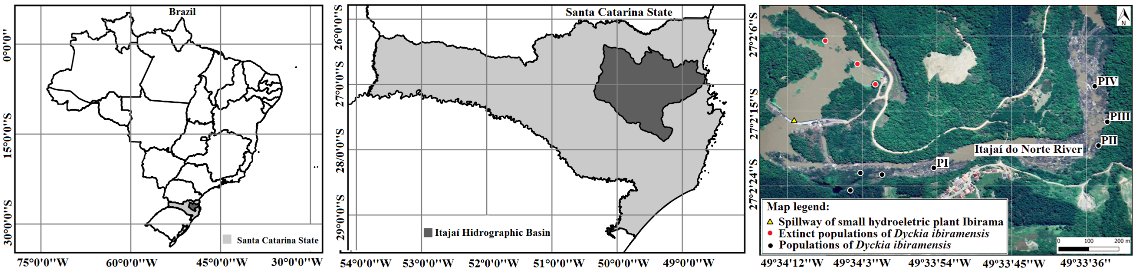

Figure 1 – Natural population distribution of *Dyckia ibiramensis* along the Itajaí do Norte River, Itajaí Hydrographic Basin, Santa Catarina state, Brazil. Organization Rosana Corazza.

populations, 13 were seedlings (0.4%), 49 rosettes occurred in isolation (1.5%) and 3,207 rosettes (98.1%) occurred in 483 clumps, totaling 3,269 rosettes (Tab. 1).

The correlation between the number of clumps and the area of occupation was positive and significant ($r = 0.99$; $P < 0.05$). The correlation between the total number of rosettes and the occupation area was also positive and significant ($r = 0.63$; $P < 0.05$).

Most isolated rosettes (73.5%) presented up to 16 cm in diameter. Only one isolated rosette was classified as reproductive (Population IV). Population II did not present any isolated rosettes (Tab. 2).

The number of rosettes per clump ranged from two to 43 and most of the clumps (87.4%) possessed up to 10 rosettes. The number of clumps per population ranged from 37 (Population III) to 237 (Population IV). Populations II and III did

Table 1 – Number of isolated and clumped rosettes per population of *Dyckia ibiramensis* Reitz, Itajaí do Norte River.

Populations	Seedlings	Isolated rosettes	Number of clumps	Total number of rosettes	Occupancy area (m^2)
Population I	5	18	170	1,255	940
Population II	-	-	39	307	2,150
Population III	-	12	37	295	30
Population IV	8	19	237	1,412	8,400
Overall	13	49	483	3,269	11,520

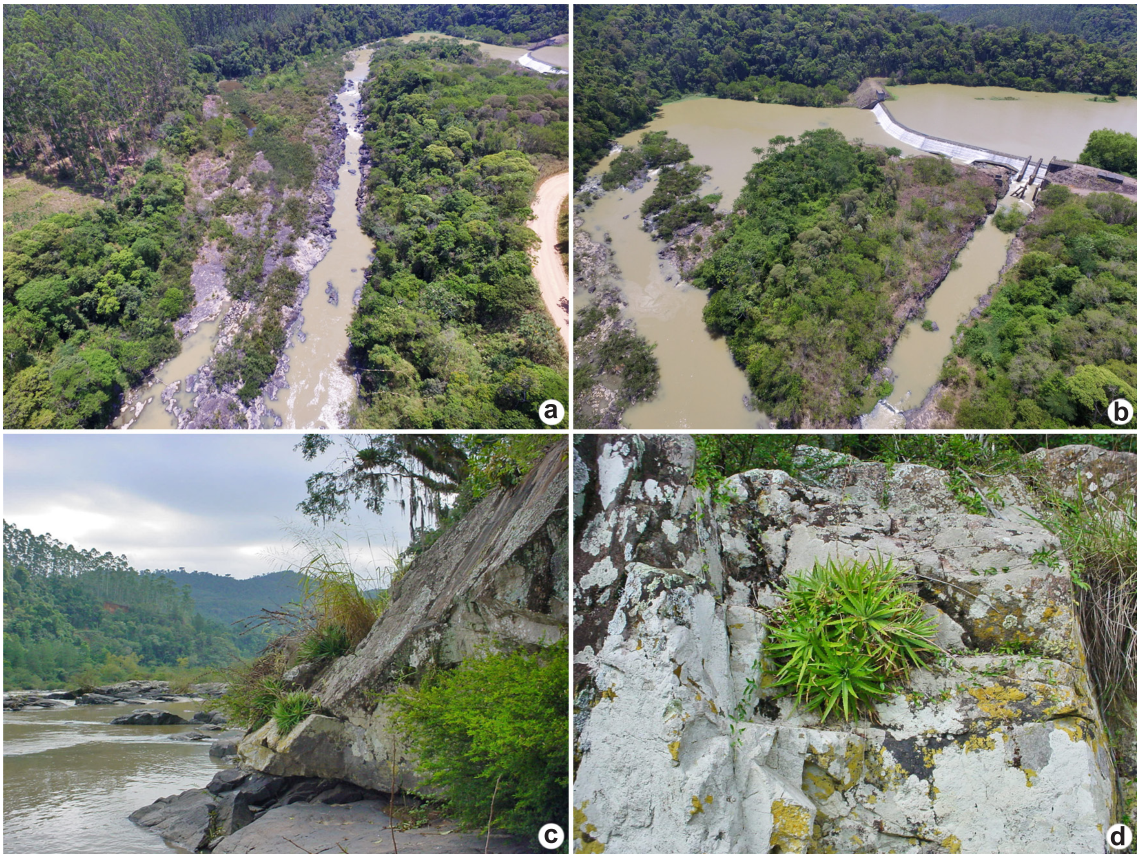

Figure 2 – Areas of occurrence of the species *Dyckia ibiramensis* in Itajaí do Norte River, Itajaí Hydrographic Basin, Santa Catarina State, Brazil – a. Occurrence habitat. b. Spillway of Ibirama small hydroelectric plant. c. Occurrence habitat of *D. ibiramensis*; d. Clump of *D. ibiramensis* on gneisses of the Santa Catarina Granulite Complex.

not present clumps with more than 30 rosettes and Population IV did not present clumps with more than 40 rosettes. The number of reproductive clumps ranged of 39.4 (Population I) to 43.6% (Population II) with an average of 41.0% (Tab. 3).

The diameter of the rosettes ranged from two to 70 cm, with an average of 20.2 ± 10.6 cm. The percentage of seedlings per population ranged from 0.4 (Population I) to 0.6% (Population IV), and Populations II e III had no seedlings. In total, 13 seedlings (0.4%) were registered. Reproductive rosettes were recorded from nine centimeters of diameter. The percentage of reproductive rosettes per population ranged from 7.8 (Population III) to 26.7% (Population II), with an average of 22.9 ± 6.3. A total of 20.3% of the rosettes were classified as reproductive. Most of the reproductive rosettes are concentrated in classes above 24 cm. The percentage of reproductive rosettes raised with the increase of rosettes diameter in all populations, with significant and positive ($P < 0.05$) Pearson's correlation (r) between these variables in all of the populations, ranging from 0.91 (Population I) to 0.96 (Population II) (Tab. 4).

Table 2 – Number and percentage (%) of seedlings and isolated rosettes per diameter class in four populations of *Dyckia ibiramensis*. Itajaí do Norte River, Ibirama, SC. *including seedling; **reproductive rosette.

Populations	Diameter classes of seedlings and isolated rosettes (cm)						Overall
	up to 8*	8-16	16-24	24-32	32-40	40-48	
Population I	10 (43.5%)	10 (43.5%)	2 (8.7%)	1 (4.3%)	-	-	23
Population II	-	-	-	-	-	-	0
Population III	4 (33.3%)	4 (33.3%)	-	2 (16.7%)	2 (16.7%)	-	12
Population IV	11 (40.7%)	10 (37%)	1 (3.7%)	3 (11.1%)	1 (3.7%)	1** (3.7%)	27
Overall	25 (40.3%)	24 (38.7%)	3 (4.8%)	6 (9.7%)	3 (4.8%)	1 (1.6%)	62

Table 3 – Number of rosettes per clump in the populations of *Dyckia ibiramensis*, Itajaí do Norte River, Ibirama, SC.

Classes of number of rosettes per clump	Number and percentage (%) of clumps per population				Overall
	I	II	III	IV	
1 (2–10)	141 (82.9)	32 (82.1)	29 (78.4)	220 (92.8)	422 (87.4)
2 (11–20)	23 (13.5)	6 (15.4)	5 (13.5)	15 (6.3)	49 (10.1)
3 (21–30)	3 (1.8)	1 (2.6)	3 (8.1)	1 (0.4)	8 (1.7)
4 (30–40)	2 (1.2)	-	-	1 (0.4)	3 (0.6)
5 (40–50)	1 (0.6)	-	-	-	1 (0.2)
Overall	170	39	37	237	483
Reproductive clumps	67 (39.4)	17 (43.6)	16 (43.2)	98 (41.4)	198 (41.0)

Among the sampled rosettes, one to three offshoots were recorded in the center of the "mother-plant" rosette. The production of offshots occurred on both immature and reproductive rosettes. The growth form presented by *D. ibiramensis* is phalanx.

Discussion

The rheophyte *D. ibiramensis* occurs in the rocky banks in areas of low flow measuring recurrence, partially or totally submerged during floods. It is seems to be a species adapted to stress (exposure rock, luminous) and ephemeral disturbances (floods and currents) (Fig. 2). In same patches that *D. ibiramensis* occurs are found the shrub species: *Calliandra selloi* (Spreng.) J.F. Macbr., *Sebastiania schottiana* (Müll. Arg.) Müll.

Arg. and *Phyllanthus sellowianus* (Klotzsch) Mull. Arg. (JM Rogalski, personal observation) that are typically rheophytes and popularly known to as 'sarandis'.

Taking into consideration the populations studied, 98.1% of the rosettes were clumped and most clumps contained few rosettes. Similar results were found for their congener rheophytes *D. brevifolia* (Rogalski & Reis 2009) and *Dyckia distachya* Hassler (JM Rogalski, unpublished data). Larger clumps may possibly be formed by combination of smaller clumps as they expand, due to their proximity, or they may also indicate older clumps.

Each rosette produced between one and three offshoots. For other bromeliads, the production of offshoots per rosette was similar and ranged from one to four offshoots per rosette (Sampaio *et al.* 2002; Mondragón *et al.* 2004; Duarte *et al.* 2007; Rogalski & Reis 2009; Fillipon *et al.* 2012; Lenzi & Paggi 2020).

A phylogenetic analysis of 2,300 clonal plants indicates that phalanx is more associated to open, dry, nutrient poor environments (van Groenendael *et al.* 1996) conditions present in the studied habitat. The phalanx growth form presented by *D. ibiramensis* is believed to be advantageous to improve resource capture as well as space occupation (Kroon *et al.* 1994), and it could also help to resist river currents during floods. In iteroparous species, like as *D. ibiramensis*, life histories and indeterminate growth and clonal expansion should lead to more flowering shoots and a greater reproductive capacity (Vallejo-Marín

Table 4 – Number of rosettes (N), percentage (%) and number of reproductive rosettes (R) per diametric class in four natural populations of *Dyckia ibiramensis*. Itajaí do Norte River.

Populations		Rosette diameter classes (cm)									Overall	*r*
		2-8	8-16	16-24	24-32	32-40	40-48	48-56	56-64	64-72		
I	N	179	336	321	262	145	12				1,255	0.91*
	R			32	74	64	4				174	
	(%)			(10.0)	(28.2)	(44.1)	(33.3)				(13.9)	
II	N	31	82	110	69	15					307	0.96*
	R		1	25	43	13					82	
	(%)		(1.2)	(22.7)	(62.3)	(86.7)					(26.7)	
III	N	44	54	50	46	64	31	4	1	1	295	0.95*
	R		1	9	22	31	16	2	1	1	82	
	(%)		(1.9)	(18.0)	(47.8)	(48.4)	(51.6)	(50.0)	(100)	(100)	(7.8)	
IV	N	297	262	338	320	184	10	1			1,412	0.95*
	R		1	21	150	149	7	1			327	
	(%)		(0.4)	(6.2)	(46.9)	(81.0)	(70.0)	(100)			(23.2)	
Overall	N	551	733	794	654	395	54	5	1	1	3,269	0.95*
	R	0	3	85	289	257	27	3	1	1	665	
	(%)	(0)	(0.4)	(10.7)	(44.2)	(65.1)	(50.0)	(60.0)	(100)	(100)	(20.3)	

et al. 2010). However, this architecture can be expected to increase geitonogameous pollination and to decrease mate availability (Charpentier 2002; Rugierro *et al.* 2005; Rogalski & Reis 2009; Rogalski *et al*. 2009). The bromeliad *D. ibiramensis* is partially self-compatible with mixed mating system (multilocus outcrossing rate ($\hat{t}_m$) ranged from 0.563 to 0.893) and shows a significant fixation index ($\hat{f}$ = 0.642) (Hmeljevski *et al.* 2011) and ($\hat{f}$ = 0.474) (Reis 2019).

The rheophyte *D. ibiramensis* has fruiting and seed dispersion in summer when the rains are frequent in late afternoon. Thus, the seeds fall on the rock by gravity and/or anemochory and are carried to the river (hydrochory). This was also verified in *D. brevifolia* by Rogalski & Reis (2009). *D. excelsa* may produce one (81%), two (17%) and three (2%) inflorescences per rosette (n = 896), and has an unusual flowering and fruiting occurring several times during a year. Also, the greatest fruiting and seed dispersion happens during the rainy season, enabling seed germination and the establishment of seedlings (Lenzi & Paggi 2020). Thus, the rain seems to play an important role in the dispersion and/or germination of the genus *Dyckia*.

At the beginning of the development of the seedlings they present only two leaves, and then, in the sequence, they increase this number until acquiring rosette shape. This step occurs up to four centimeters in diameter and these plants were considered seedlings. High natural fructification (89%) and high germination (94%) in greenhouse conditions on vermiculite substrate (Hmeljevski *et al.* 2011) were registered in these same populations, though only 0.4% of seedlings were registered in natural conditions in this study. Our results suggests the occurrence of "bottlenecks" associated with germination, establishment and recruitment of individuals, which can be caused mainly by the environmental selectivity of this species, since they occur in patches with favorable conditions and in this stress habitat.

Otherwise, seedlings and isolated rosettes (1.9%) were originated from seeds. It is important to point out that the species studied is perennial, iteroparous and presents clonal propagation. These characteristics are very important for the maintenance, in the long-term, of genets in populations. Clonal propagation could make up for low seedling recruitment (Seligman & Henkin 2000; Arizaga & Ezcurra 2002) since reducing the risk of genets mortality through ramets (Cook 1985; Eriksson 1993).

Some studies with bromeliads either did not find seedlings (Sampaio *et al.* 2005), or found that they were very rare (García-Franco 1990; Villegas 2001; Zaluar & Scarano 2000; Duarte *et al.* 2007; Fillipon *et al.* 2012; García-Meneses & Ramsay 2014). In other bromeliads, clonal propagation predominated over sexual reproduction (García-Suarez *et al.* 2003; Hietz *et al.* 2002). In *Tillandsia brachycaulos* Schltdl. (Mondragón *et al.* 2004), in *Aechmea distichantha* Lem. (Barberis *et al.* 2020) and in *D. brevifolia* (Rogalski & Reis 2009; Rogalski *et al.* 2017), the main recruitment mechanism for new individuals was clonal propagation, although seedling recruitment occur frequently. In *Neoregelia johannis* (Carrière) L.B. Sm. the recruitment rate was similar in both forms (Cogliatti-Carvalho & Rocha 2001). Nevertheless, the vegetative reproduction has no effect on the life cycle of the *Werauhia sanguinolenta* (Cogn. & Marchal) J.R. Grant (Zotz *et al.* 2005). In addition, clonal propagation was not recorded in *Puya hamata* L.B. Sm. plants (García-Meneses & Ramsay 2014) and it was very low in *Dyckia excelsa* Leme (Lenzi & Paggi 2020). Thus, in the Bromeliaceae family the balance between sexual reproduction and clonal propagation differs between species.

Our results confirm Harper's review (1977) of the dynamics of perennial herbaceous populations, suggesting that recruitment via seeds contributes little to the maintenance of populations. Plants with sexual origin have a higher mortality rate and lower levels of success in the establishment (Zhang & Zhang 2007). According to Mondragón *et al.* (2004), even though seedlings are produced annually a substantial recruitment occurs only in favorable years. Moreover, these authors reported that mortality is higher in the early stages of development and that sexually produced individuals are more vulnerable. In some species of bromeliads, the probability of seedlings becoming reproductive, after germination and establishment, ranges from 2.8 to 5% (Hietz *et al.* 2002). However, in *Vriesea gigantea* Gaudich. the recruitment of seedlings was high with 72.4% becoming adults (Paggi 2009).

In Andean *Puya* (Bromeliaceae) temperature fluctuations, ice crystal formation, solifluction and intense solar radiation are factors that limit seedling establishment (Jabaily & Sytsma 2013). Drought was considered the main cause of death during the early stages of development of epiphytic bromeliads (Benzing 1981; Mondragón *et al.* 2004;

Zotz *et al.* 2005), as well, very low temperatures in *A. distichantha* (Barberis *et al*. 2020). In the case of *D. ibiramensis*, besides lack of water, lack of nutrients and floods may also cause death, because they are not yet attached to the rock. In *D. duckei* L.B. Sm. and *D. racemosa* Baker seedlings accumulate little water between their leaves (Silva & Scatena 2011), possibly requiring more water in this stage. For most *bromeliads*, aridity and low levels of nutrient availability represent the primary causes of stress in all life history stages (Hernández *et al.* 1999; Benzing 2000).

Clonal propagation makes it harder to determine the number of genets present in populations. The high percentage of clumped rosettes could indicate that clonal propagation prevails in the species, possibly suggesting that the clumps are mainly made up of ramets. On the other hand, different clumps, isolated rosettes and seedlings could be considered genets. Thus, the populations I, II, III and IV would have at least 193, 39, 49 and 264 genets, respectively. In this same populations different clumps were evaluated by allozyme markers indicating an intermediate genetic diversity (mean $\hat{H}_E$ = 0.219; 0.094, Hmeljevski *et al.* 2011; Reis 2019, respectively) showing that not are clones. Considering only the reproductive ones (without considering the genetic diversity within of clumps, the matings, and the evolutionary factors) one isolated rosette and 198 clumps (41.0%) had reproductive rosettes, totaling only 199, if the clumps consist only of clones, which is a very small size.

The low number of seedlings and isolated rosettes (totaling 62) could indicate that the species generates few individuals sexually. However, it is important to point out that this study was carried out in a single moment, which may have been a disadvantage for germination and seedling development. Sexual reproduction is the main factor to determine the formation of new genets and it is important to determine the population genetic structure (Amat *et al.* 2013). The sexual reproduction (increasing the genet number) and clonal propagation (maintained and spread the genet) presented for *D. ibiramensis* may be an advantage in this unstable environment. Clones are prone to habitat instability.

The relative proportions of sexual *vs*. asexual progeny generated may often vary widely within a species, due to variations in ecological and/or genetic factors that limit or enhance reproductive modes (Eckert 2002). Most perennial herbaceous can reproduce vegetatively suggesting that clonality may be a common feature of this group (Richards 1997) and in the species of Bromeliaceae family (Benzing 2000) with consequences such as recruitment and population maintenance (Villegas 2001).

Regarding the demographic structure, the diameter of rosettes gives an idea of how old they are. However, clones show faster growth and they require less time to become reproductive (Benzing & Davidson 1979; Ticktin *et al.* 2003; Mondragón *et al.* 2004). Even though the growth rate of *P. hamata* varied according to rosette size, there was little variation in the size of reproductive rosettes (García-Meneses & Ramsay 2014)**.** Besides, it is likely that the variation in rosette size of the species also occurs as a function of light intensity (fully exposed or in shadow of the sarandis). For vegetative ramets, plant survival was higher in the shade than in the sun; and the higher flowering of ramets in the shade is probably associated with milder conditions in the understory (Barberis *et al*. 2020).

In *D. ibiramensis*, the larger the diameter of the rosettes, the greater the probability of becoming reproductive. In other species of bromeliads, the number of reproductive individuals also increased with the increment of plant size (Benzing 1981; Hietz *et al.* 2002; Mondragón *et al.* 2004; Duarte *et al.* 2007; Rogalski & Reis 2009; Fillipon *et al.* 2012).

In *D. ibiramensis*, the offshoot production occurred in plants of different diameters despite sexual reproduction, which was also observed in *D. brevifolia* (Rogalski & Reis 2009; Rogalski *et al.* 2017) and *D. distachya* (JM Rogalski unpublished data). In *Bromelia pinguin* L. and *Aechmea nudicaulis* (L.) Griseb., the production of offshoots also happens in spite of sexual reproduction, usually before flowering (Garcia-Franco & Rico-Gray 1995; Sampaio *et al.* 2002). On the other hand, in *Tillandsia circinnata* Schltdl., the production of offshoots begins when the mother-plant starts to produce inflorescence (Benzing 2000). In *A. distichantha* ramet production was higher for reproductive ramets and very low for young ones (Barberis *et al*. 2014) and *Vriesea neoglutinosa* Mez produces offshoots only after sexual reproduction (Sampaio *et al.* 2002). In bromeliads, clonal propagation is not restricted to adults and not all reproductive adults produce offshoots (Benzing 1980).

Clonal propagation is a common feature in perennial herbaceous and may be extremely important for species living in harsh environments both for recruitment and maintenance of populations. Moreover, in endemic species with few populations, such as *D. ibiramensis*, it may be essential for the maintenance of genetic diversity. According Rogalski *et al*. (2017) it manly occurs due to founder event (few individuals found new population), endogamy (mixed reproductive system) and genetic drift (small and disjunctive populations). Despite the short distance between the *D. ibiramensis* populations (Tab. 1), they present high genetic divergence (G_{ST} = 0.674; Hmeljevski *et al.* 2011), indicating low gene flow among populations.

According to Abrahamson (1980), the balance between sexual reproduction and clonal propagation has a great influence on population demography. It is likely that most rosettes in initial diameter classes are clones, since few isolated rosettes and seedlings were observed. However, this is a cross-sectional study and, according to Mondragón *et al.* (2004), longitudinal studies are necessary in order to properly describe the demographics of long-lived species, since populations may vary over the years.

The structure of plant populations results from the action of biotic and abiotic factors on their current and ancestor members, which affect the spatial arrangement and age/genetic structures of its components (Hutchings 1997). In the studied populations, *D. ibiramensis* was characterized by few seedlings and isolated rosettes, forming small clumps with ample variation in the number of rosettes per clump and of the number of clumps per population. This variation probably occurs as a function of the area of available occupation (see Tab. 4) and the time of colonization of each place. Besides these factors, the form of recruitment (via sexual reproduction and/or vegetative propagation) in the populations seems to be determinant for the demographic structure of this species.

D. ibiramensis is perennial, iteroparous and presents clonal propagation what seem to be important for the maintenance of the populations of this species in this habitat, additionally few individuals are recruited sexually. The clonal propagation may be extremely important considering that *D. ibiramensis* occurs in an environment with harsh conditions (luminous, exposed rock, flood, stream), for both formation and the maintenance of its populations. In places exposed to flooding, many perennial herbaceous plants show clonal propagation, which contributes to their permanence in such environments (Menges & Waller 1983; Prach & Pysek 1994; Rogalski & Reis 2009; Rogalski *et al.* 2009).

An example not to be repeated with *D. ibiramensis* is that of rheophyte *D. distachya* which occurred in Uruguay River in state´s border of Santa Catarina and Rio Grande do Sul, Southern Brazil. The species also had a disjunctive distribution, occurring in 617 km, from Pelotas River (tributary of the Uruguay River) to Salto do Yucumã in Uruguay River (border of Brazil and Argentine). Seven of its eight populations were extinct in nature due to the construction of the Hydroelectric Power Plants of Itá, Machadinho, and Barra Grande.

Part of the flooded populations of *D. distachya* were rescued and kept in nurseries, and after that, were reintroduced in the regions close to their areas of occurrence (Wiesbauer & Zimmermann 2011). In this case, of the 20 places where they were reintroduced at, only four (Vacas Gordas River, Uruguay Basin) the plants persisted and are reproducing and regenerating (Wiesbauer & Zimmermann 2011). These authors reported as the main difficulties in reintroduce this species the great difficulty in fixing the rosettes of *D. distachya* on the rock, the herbivory and furthermore, several times the plants were carried by water.

The plants that were rescued, before the immersion of the populations of *D. ibiramensis* by small hydroelectric plant of Ibirama, were reintroduced in the three more close populations. Most plants persisted for many years but all ended been carried by the floods and no reintroduced plants remained.

In the studied cases, the bromeliads *D. distachya* and *D. ibiramensis* showed that the reintroduction of rheophytes is very difficult as well as indicated that there is a high risk to plan the conservation of these species only via *inter* and *ex situ*. The three forms of conservation (*in*, *ex* and *inter situ*) can be the best strategy for rheophyte species.

In the case of *D. ibiramensis*, studies aiming to clarify the genetic diversity within clumps may help to estimate the population size more accurately. In addition to this, the long-term monitoring of populations (demography, phenology, reproduction, and genetic) may contribute to better understand: germination, establishment and recruitment of individuals; the formation of clumps; the growth of rosettes;

and how large floods affect the populations. The dynamics of these populations need to be studied for a long time which will contribute to define conservation strategies.

Few seedlings and isolated rosettes, production of offshoots occurred on both immature and reproductive rosettes with one to three clones, and clumps with few rosettes can indicate the clonal propagation as the main reproduction form in *D. ibiramensis*. In future, if more populations are affected, *ex situ* conservation needs to be carried out following the recommendations of collection of rosettes and/or seeds suggested by Hmeljevski *et al*. (2011). For reintroduction of plants, the *inter situ* conservation can follow the recommendations of Wiesbauer & Zimmermann (2011).

The high degree of endemism shown by *D. ibiramensis*, its small area of occupation and the low number of clumps with reproductive rosettes make this species very vulnerable. Therefore, the maintenance and the monitoring of their populations are essential for its long-term *in situ* conservation.

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