

Original Article

## Demographic structure across all known populations of the rheophyte *Dyckia brevifolia* Baker (Bromeliaceae) in the Itajaí-Açu River, Southern Brazil

Estrutura demográfica de todas as populações conhecidas da reófito *Dyckia brevifolia* Baker (Bromeliaceae) no Rio Itajaí-Açu, Sul do Brasil

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### Abstract

Understanding the distribution and demographic structure of populations is essential for species conservation. In Brazil, the rheophyte group has been greatly affected by the construction of hydroelectric dams. All known populations of *Dyckia brevifolia* Baker along Itajaí-Açu River were studied. The plants were classified as seedlings, immature or reproductive rosettes. In addition, the number of dead rosettes, except for seedlings, was determined in five populations of *D. brevifolia*. The total number of rosettes per population ranged from 273 to 7,185, totaling 30,443 rosettes, and 1,789 seedlings (5.9%). Only 2.4% of rosettes occurred isolated and 97.6% occurred clumped into 2,254 clumps. The number of rosettes per clump ranged from two to 339 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 ( $r = 0.82$ ;  $P < 0.05$ ). The production of offshoots (1–4) occurred on immature and reproductive rosettes. *Dyckia brevifolia* has herbivory by *Hydrochaeris hydrochaeris* (capybara). These rosettes die or often resprout, emitting from 1 to 20 shoots. The populations did not present a pattern of distribution of rosettes in the diametric classes, but in all populations a decrease in the number of rosettes can be observed in the classes with the largest diameter. The small area of occupation (9,185 m<sup>2</sup>) showed high environmental specificity and vulnerable to habitat loss and environmental changes. Therefore, the maintenance these sites is essential for the long-term conservation of *D. brevifolia*.

**Keywords:** demography, herbivory by capybara, clonal propagation, endemic species, polycarpic.

### Resumo

Compreender a distribuição e a estrutura demográfica das populações é essencial para a conservação das espécies. No Brasil, o grupo reófitas tem sido muito afetado pela construção de hidrelétricas. Todas as populações conhecidas de *Dyckia brevifolia* Baker ao longo do Rio Itajaí-Açu foram estudadas. As plantas foram classificadas como plântulas, imaturas ou rosetas reprodutivas. Além disso, o número de rosetas mortas, exceto plântulas, foi determinado em cinco populações de *D. brevifolia*. O número total de rosetas por população variou de 273 a 7.185, totalizando 30.443 rosetas e 1.789 plântulas (5,9%). Apenas 2,4% das rosetas ocorreram isoladas e 97,6% ocorreram agrupadas em 2.254 touceiras. O número de rosetas por grupo variou de duas a 339 rosetas. A porcentagem de rosetas reprodutivas por população variou de 7,8 a 26,7%. A correlação entre o número de touceiras ou entre o número total de rosetas e a área de ocupação foi significativa e positiva ( $r = 0,82$ ;  $P < 0,05$ ). A produção de brotos (1–4) ocorreu em rosetas imaturas e reprodutivas. *Dyckia brevifolia* tem herbivoria por *Hydrochaeris hydrochaeris* (capivara). Essas rosetas morrem ou muitas vezes rebrotam, emitindo de 1 a 20 brotos. As populações não apresentaram um padrão de distribuição de rosetas nas classes diamétricas, mas em todas as populações pode ser observada uma diminuição no número de rosetas nas classes de maior diâmetro. A pequena área de ocupação (9.185 m<sup>2</sup>) mostrou especificidade ambiental e vulnerabilidade à perda de habitat e alterações ambientais. Portanto, a manutenção desses locais é essencial para a conservação em longo prazo de *D. brevifolia*.

**Palavras-chave:** demografia, herbivoria por capivaras, propagação clonal, espécie endêmica, policarpia.

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## 1. Introduction

In Brazil, Bromeliaceae Juss. is one of the most important families (1,392 species with 85.6% of endemism and 54 genera) (JBRJ, 2023). In ecological terms, bromeliads may be described as a group of (luminous, hydric and nutritional) stress-tolerant tropical herbs with an accentuated tendency to epiphytism and occupation of rupestrian environments (Benzing, 1980). The more than 3,000 bromeliad species that currently occupy the Neotropical region have evolved to fill numerous niches, with an incredible diversity of adaptations (Zanella et al., 2012). In restingas, complex areas favor the occurrence of more bromeliad species, due to the greater availability of microhabitats (Rocha-Pessôa et al., 2008). Considerations of the clonal and sexual reproduction, demography, genetic structure within and among populations, gene flow, and mating systems of Bromeliaceae are of primary importance in developing successful conservation strategies (Bizoux and Mahy, 2007).

In Brazil, the genus *Dyckia* Schult. & Schult. f. presents 164 species, of these 154 endemics (Guarçoni et al., 2023). According to Klein (1979), some bromeliad species of the genus *Dyckia* occur as rheophytes. The occurrence of rheophytes is linked to the presence of swift-running rivers (van Steenis, 1981). Rheophytes has a greater richness of taxa in the obligatory category, was found mainly in southern Mexico, southern Brazil, Central Africa (Cameroon and Gabon), Madagascar, East (southern China) and Southeast Asia (Borneo), and northern Australia (Kimberley and Northern Territory) (Costa et al., 2020).

Currently many water resources have been exploited with great human interventions on the regime and course of these water bodies (Rosenberg et al., 2000). The construction of dams for energy generation and water collection for urban and rural supply, as well as water channeling, have had a negative impact on the quality and availability of water, and on the maintenance of the life of natural systems (Moulton and Souza, 2006). According to the Agência Nacional de Energia Elétrica, the Brazil has in operation 219 large hydroelectric power plants, 425 small hydroelectric power plants and 739 hydroelectric power stations (ANEEL, 2022). Due the installation of the Salto Pilão hydroelectric power plant, part of the two populations of the *Dyckia brevifolia* Baker in the municipality of Lontras, Santa Catarina State, southern Brazil, already were affected by the formation of the lake. The forecast of the construction of other small hydroelectric power plants puts many rheophytes and riparian species at risk of extinction.

This study aimed to know the population structure of the rheophyte *D. brevifolia* and its distribution. It is of paramount importance to draw attention to this biological group, practically unstudied, which has been very affected with hydroelectric power plants. According to Freitas et al. (2020), for rare and endemic bromeliads more data are needed (e.g. counts or estimates of the total abundance) to respond concretely if the current populations are sufficient for the long-term survival of species.

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 number of seedlings per population, (iv) what is the main form of occurrence of the rosettes (isolated or clumped), (v) what is the number of rosettes per clump, (vi) what correlation might exist between rosette size (diameter) and sexual reproduction, (vii) how many clumps had reproductive rosettes, and (viii) 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 all known natural populations of *D. brevifolia* across the Itajaí- Açú River. In addition, in five populations of this species we asked (ix) what is the number of rosettes died, except for seedlings.

## 2. Material and Methods

*Dyckia brevifolia* Baker (Bromeliaceae) – The rheophyte *D. brevifolia* occur along Itajaí-Açú River (Rogalski et al., 2007a; Rogalski and Reis, 2009). *Dyckia brevifolia* has an outcrossing rate of 8.2%, with predominant selfing and mixed pollination, being pollinated by the hummingbird *Amazilia versicolor* Vieillot (main pollinator) and by bees of the genera *Xylocopa* and *Bombus* (Rogalski et al., 2007b; Rogalski et al., 2009). The mean expected genetic diversity was 0.067 and downstream populations along Itajaí-Açú River showed the highest genetic diversity which could be attributed to hydrochory (unidirectional river flow). Most genetic diversity is distributed among populations ( $F_{ST} = 0.402$ ) (Rogalski et al., 2017).

*Study area* – The Itajaí River Basin has 15,500 km<sup>2</sup>, which corresponds to approximately 16% of the territory of the Santa Catarina State, Southern Brazil. By considering its natural characteristics, the Itajaí hydrographic basin may be divided into: upper, middle and lower Itajaí Valley (SIRHESC, 2023). The regional climate, according to Köppen classification, is subtropical *Cfa* type with an annual average temperature of 18.5°C, annual rainfall between 1,300 and 1,500 mm, and constant rainfall in the summer (Collaço, 2003).

The species occurred in areas of low water recurrence on the banks or within the larger river bed, in places with rapids and strong, which leaves the exposed rocks without sediment deposit. During the floods the sites are partially or completely submerged.

Throughout its distribution, 12 sites (Ressacada, Subida/Apiúna I, Subida/Apiúna II and Subida/Apiúna III, in the municipality of Apiúna; Subida/Ibirama I, Subida/Ibirama II and Morro Santa Cruz in the municipality of Ibirama; Ascurra in the municipality of Ascurra; Encano Baixo and Encano in the municipality of Indaial; Salto Waissbach I and Salto Waissbach II in the Blumenau municipality) with occurrence of *D. brevifolia* were recorded and studied (Figure 1), according Rogalski et al. (2021).

The area of occupation of the species in each location was determined from the extreme limits of its occurrence. Each set of isolated and grouped rosettes present in a given location was considered as a population.

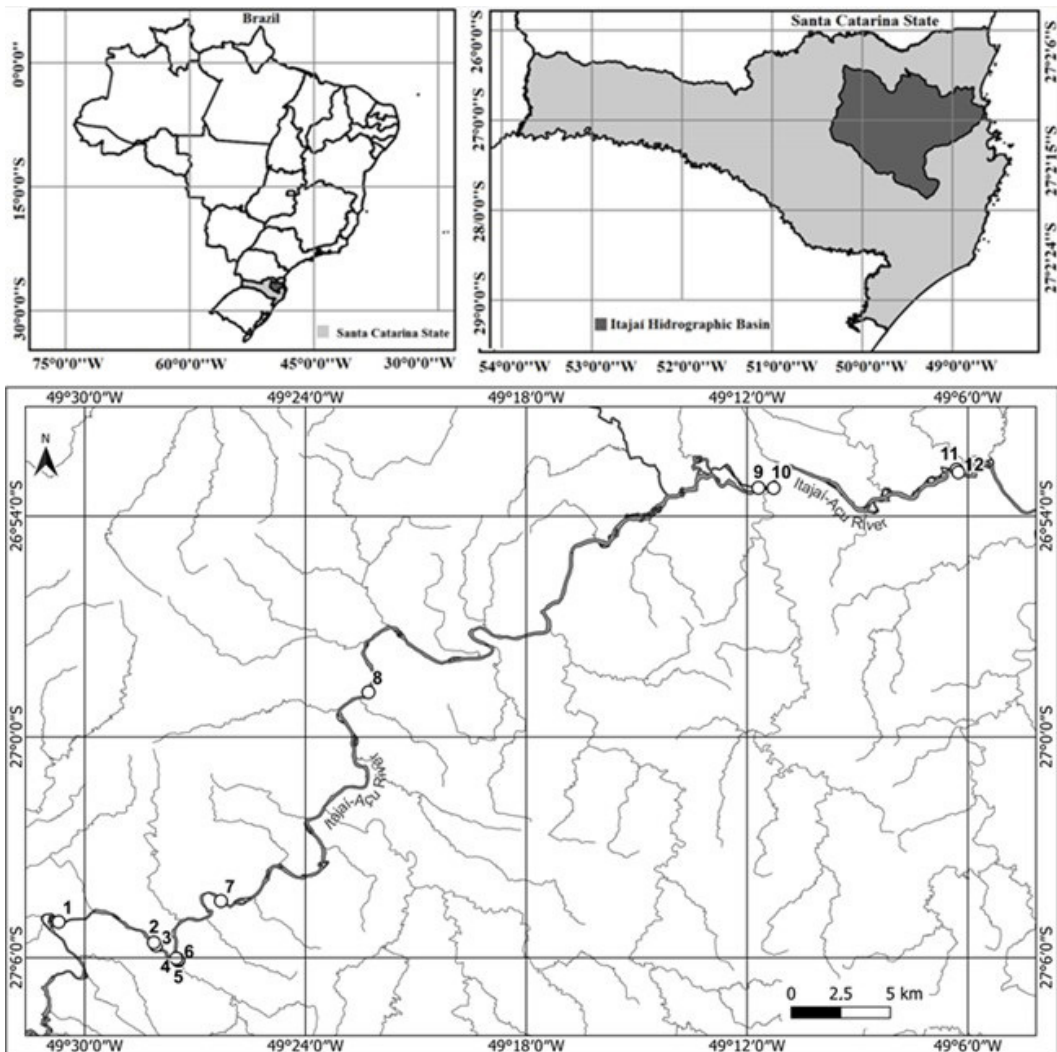
Regarding the classification of the stage of development of rosettes, the following were considered: seedlings that contained only two leaves; immature ones that presented rosette form and showed no signs or presence of inflorescence and/or fruits; and reproductive ones that had a rosette shape and had signs or presence of inflorescence and/or fruit. Regarding the form of occurrence, the rosettes were classified as isolated rosette or clumped.

In each population, the count of all rosettes was performed, and the largest diameter of each rosette was measured, except for the seedlings. The data obtained for each population were distributed in diameter classes of leaf rosettes (centimeters), for all stages of development (seedling, immature and reproductive rosette). Seedlings were included in the class up to 5 cm in diameter.

Data adherence to normal ( $p < 0.05$ ) was tested for each population using the STATISTICA 6.0 Program.

Pearson's correlations were estimated between the total number of rosettes and the area occupied by *D. brevifolia*; and between the percentage of reproductive rosettes and the center of each diameter class, according to Steel and Torrie (1980).

The forms of vegetative propagation presented by *D. brevifolia* were evaluated. Vegetative propagation (clonal) was evaluated in a single moment in five populations (Subida/Apiúna I; Subida/Apiúna II; Subida/Ibirama I; Morro Santa Cruz/Ibirama; and Encano/Indaial), being recorded the number of axillary offshoots. In addition, it was verified whether the rosette was reproductive. In these five populations, rosette mortality was also evaluated at a single time, except for seedlings.



**Figure 1.** Populations studied of *Dyckia brevifolia* Baker, Itajaí-Açu River (SC). (1) Ressacada; (2) Subida/Apiúna I; (3) Subida/Ibirama I; (4) Subida/Apiúna II; (5) Subida/Apiúna III; (6) Subida/Ibirama II; (7) Morro Santa Cruz; (8) Ascurra; (9) Encano Baixo; (10) Encano; (11) Salto Waissbach I; (12) Salto Waissbach II. Organization Rosana Corazza. In figure on the left, Brazil indicating in light gray the state of Santa Catarina. In the figure on the right, in light gray State of Santa Catarina and in dark gray Itajaí hydrographic basin. In the figure below, in dark gray Itajaí-Açu River indicating the registered populations and in light gray tributaries.

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.

### 3. Results

The highest concentration of populations occurred near the confluence of the Itajaí-Açu and Hercílio Rivers, in the municipalities of Apiúna and Ibirama (Figure 1). The rheophyte *D. brevifolia* has an extension of occurrence of about 80 km along the Itajaí-Açu River, from Lontras to Blumenau, Southern Brazil (Figure 2).

The populations of *D. brevifolia* showed disjunct distribution and in the 12 populations studied, their area of occupation was 9,185 m<sup>2</sup>, that is, less than one hectare. In the 12 populations studied, 30,443 rosettes were registered, and the number of rosettes ranged from 204 (Salto Waissbach II) to 7,185 (Subida/Ibirama I). Rosette density per population ranged from 0.4 (Subida/Ibirama II) to 6.6 rosettes per m<sup>2</sup> (Subida/Apiúna I), with an average of  $3.5 \pm 1.9$  rosettes

per m<sup>2</sup> (Table 1). There is a significant positive correlation between the area occupied by *D. brevifolia* and the total number of rosettes ( $r = 0.82$ ;  $P < 0.05$ ).

*Dyckia brevifolia* occurred on rocks of the Gneiss types of the Archean (Santa Catarina Granulitic Complex) and rhyolites of the Proterozoic Superior (Itajaí Group, Campo Alegre Formation). In both lithotypes, the species was predominantly on non-meteorized rock, however, in rock disjunctions (fractures, failures and decompression plates).

Only 722 rosettes (2.4%) occurred isolated and 29,721 (97.6%) occurred clumped into 2,254 clumps (Table 2). The number of clumps per population ranged from 13 (Salto Waissbach II) to 686 (Subida/Ibirama I) (Table 2).

The clumps consisted only of *D. brevifolia* or, sometimes, the species was associated with shrubby species: *Calliandra selloi* (Spreng.) J.F. Macbr., *Sebastiania schottiana* (Müll. Arg.) Müll. Arg., *Phyllanthus sellowianus* (Klotzsch) Müll. Arg., and *Raulinoa echinata* R.S.Cowan. The number of rosettes per clump ranged from two to 339. Most clumps (68.3%) consist of up to 10 rosettes and only 25 groups (1.1%) contained more than 100 rosettes (Table 3).



**Figure 2.** *Dyckia brevifolia* Baker in its natural habitat, Itajaí-Açu River (SC).

**Table 1.** Geographic coordinates (UTM), number of rosettes, occupied area and density (rosettes per square meter) of *Dyckia brevifolia* Baker (Bromeliaceae) for each population studied, Itajaí-Açu River (SC).

Populations	Geographic coordinates (UTM)	Number of rosettes	Area (m <sup>2</sup> )	Density (rosettes per m <sup>2</sup> )
Ressacada	(22J) 0647547, 7003408	606	150	4.0
Subida/Apiúna I	(22J) 0651906, 7002176	4,860	736	6.6
Subida/Ibirama I	(22J) 0651815, 7002320	7,185	1,302	5.5
Subida/Apiúna II	(22J) 0652896, 7001402	2,308	432	5.3
Subida/Ibirama II	(22J) 0652798, 7001515	273	630	0.4
Subida/Apiúna III	(22J) 0652902, 7001462	5,773	2,296	2.5
Morro Santa Cruz	(22J) 0654850, 7004371	4,702	2,400	2.0
Ascurra	(22J) 0661614, 7014765	664	286	2.3
Encano Baixo	(22J) 0679296, 7024784	467	195	2.4
Encano	(22J) 0679980, 7024765	508	200	2.5
Salto Waissbach I	(22J) 0688230, 7025570	2,893	486	6.0
Salto Waissbach II	(22J) 0688305, 7025431	204	72	2.8
Total	-	30,443	9,185	42.3
Mean	-	2,536.9	765.4	3.5
Standard deviation	-	2,496.3	811.6	1.9

A total of 1,789 seedlings (5.9%) were recorded in the 5 populations studied, with an average of  $149.1 \pm 202.6$  seedlings per population (Table 4). In two populations (Encano Baixo and Salto Waissbach II) no seedling was recorded. On average, 77.9% of the rosettes were immature and these predominated in all populations studied (Table 4). Sexual reproduction was observed in rosettes from 9 cm of diameter. The average percentage of reproductive rosettes was of  $13.6\% \pm 5.9$ , ranged from 4.1 (Encano Baixo) to 20.4% (Subida/Apiúna II) (Table 4). None isolated rosette was reproductive.

The populations did not present a pattern of distribution of rosettes in the diametric classes, but in all populations a decrease in the number of rosettes can be observed in the classes with the largest diameter (Figure 3). Only the

Encano Baixo population adhered to normal distribution ( $\chi^2 = 2.847$ ;  $P < 0.05$ ). The correlation between the percentage of reproductive rosettes and the diameter of rosettes was positive and significant in all populations (ranging from 0.84 to 0.98;  $p < 0.01$ ), except for Salto Waissbach II. Considering all populations studied, the correlation between these variables was also positive and significant ( $r = 0.97$ ;  $p < 0.01$ ) (Table 5).

The recruitment of new rosettes in the populations occurred through the entry of seedlings (sexual reproduction) and offshoots (vegetative propagation); and the clonal emission occurred in both immature and reproductive rosettes. Rosette mortality (output) occurred in all phases but it was not evaluated in seedlings (Figure 4).

**Table 2.** Number of rosettes isolated and grouped by population of *Dyckia brevifolia* Baker (Bromeliaceae), Itajaí-Açu River, (SC).

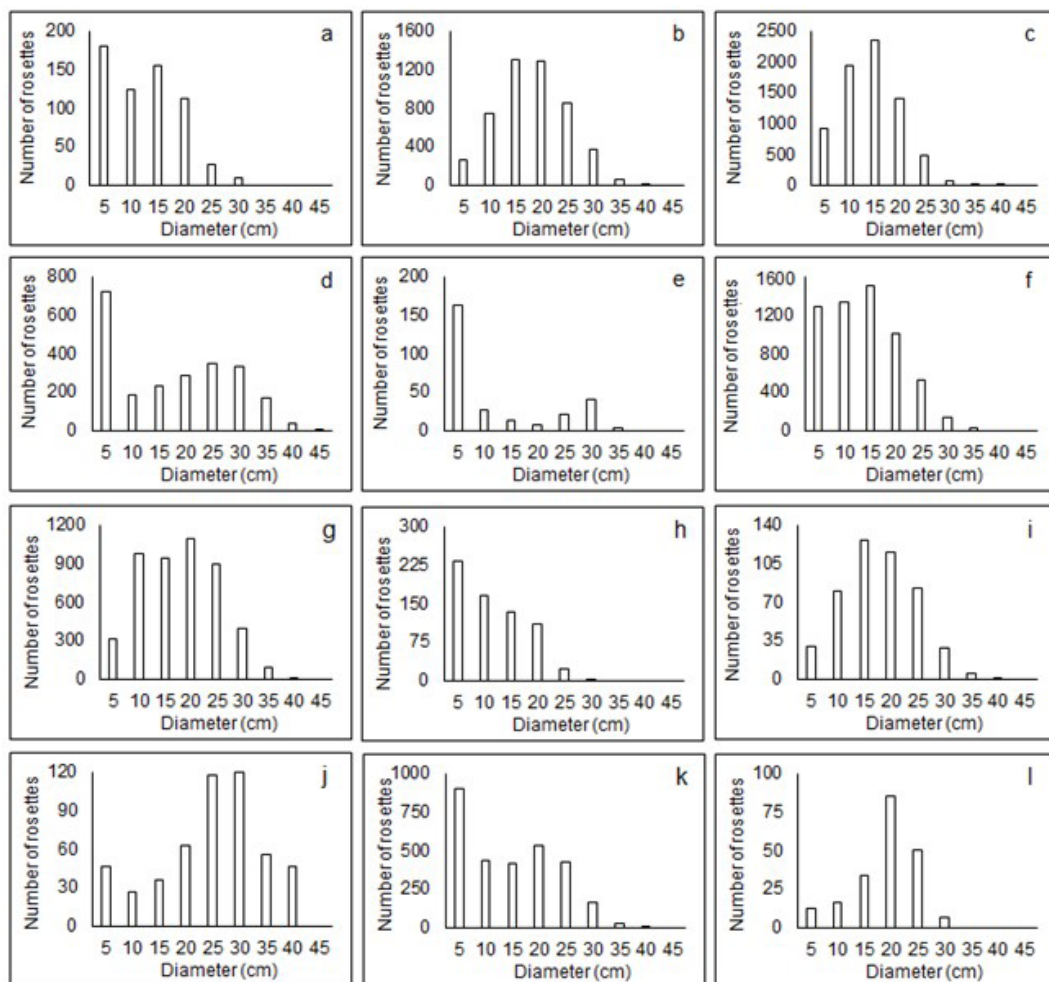
Populations	Isolated rosette	Rosettes clumped	Number of clumps	Total number of rosettes
Ressacada	7	599	39	606
Subida/Apiúna I	56	4,804	249	4,860
Subida/Ibirama I	195	6,990	686	7,185
Subida/Apiúna II	24	2,284	98	2,308
Subida/Ibirama II	23	250	25	273
Subida/Apiúna III	105	5,668	394	5,773
Morro Santa Cruz	112	4,590	318	4,702
Ascurra	84	580	58	664
Encano Baixo	5	462	40	467
Encano	14	494	37	508
Salto Waissbach I	95	2,798	297	2,893
Salto Waissbach II	2	202	13	204
Total	722	29,721	2,254	30,443

**Table 3.** Number of rosettes per clump in 12 populations of *Dyckia brevifolia* Baker (Bromeliaceae), Itajaí-Açu River (SC).

Populations	Number of rosettes				Total number of clumps
	up to 10	11-50	51-100	>100	
Ressacada	27	9	2	1	39
Subida/Apiúna I	142	88	14	5	249
Subida/Ibirama I	502	169	13	2	686
Subida/Apiúna II	55	32	6	5	98
Subida/Ibirama II	18	6	1	-	25
Subida/Apiúna III	245	133	13	3	394
Morro Santa Cruz	218	85	8	7	318
Ascurra	42	15	1	-	58
Encano Baixo	25	14	1	-	40
Encano	25	9	3	-	37
Salto Waissbach I	232	57	6	2	297
Salto Waissbach II	8	3	2	-	13
Total	1,539 (68.3%)	620 (27.5%)	70 (3.1%)	25 (1.1%)	2,254

**Table 4.** Classification of the development stage of rosettes in 12 populations of *Dyckia brevifolia* Baker (Bromeliaceae), Itajaí-Açu River (SC).

Populations	Number (N) and percentage (%) of seedlings and rosettes						Total
	Seedlings		Immatures		Reproductives		
	N	%	N	%	N	%	
Ressacada	56	9.2	441	72.8	109	18.0	606
Subida/Apiúna I	20	0.4	3,867	79.6	973	20.0	4,860
Subida/Ibirama I	133	1.9	6,052	84.2	1,000	13.9	7,185
Subida/Apiúna II	632	27.4	1,206	52.3	470	20.4	2,308
Subida/Ibirama II	107	39.2	125	45.8	41	15.0	273
Subida/Apiúna III	361	6.3	5,068	87.8	344	6.0	5,773
Morro Santa Cruz	24	0.5	3,847	88.5	831	17.7	4,702
Ascurra	54	8.1	545	82.1	65	9.8	664
Encano Baixo	0	-	448	95.9	19	4.1	467
Encano/Indaial	12	2.4	394	77.6	102	20.1	508
Salto Waissbach I	390	13.5	2,212	76.5	291	10.1	2,893
Salto Waissbach II	0	-	188	92.2	16	7.8	204
Mean	149.1	10.9	2,032.8	77.9	355.1	13.6	2,536.9
Total	1,789	5.9	24,393	80.1	4,261	14.0	30,443

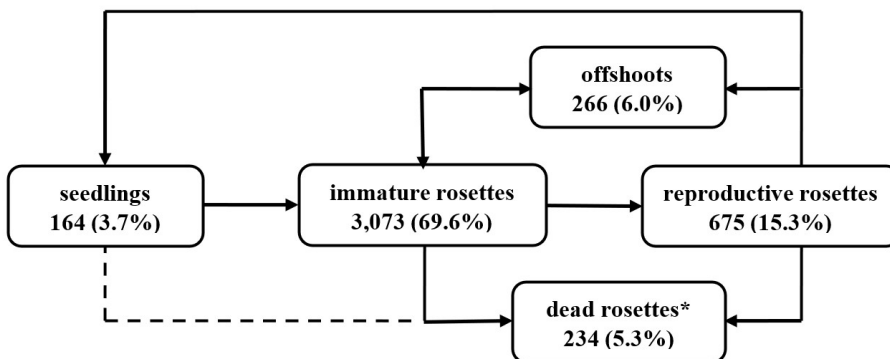


**Figure 3.** Number of rosettes per diameter class of the rosette (cm) in 12 populations of *Dyckia brevifolia* Baker (Bromeliaceae), Itajaí-Açu River (SC). The class up to 5 cm of diameter includes seedlings. (a) Ressacada; (b) Subida/Apiúna I; (c) Subida/Ibirama I; (d) Subida/Apiúna II; (e) Subida/Apiúna III; (f) Subida/Ibirama II; (g) Morro Santa Cruz; (h) Ascurra; (i) Encano Baixo; (j) Encano; (k) Salto Waissbach I; (l) Salto Waissbach II.

**Table 5.** Number (N) and percentage (%) of reproductive rosettes per diametric classes and Pearson's correlation (*r*) between the diameter of the rosette and the percentage of reproductive rosettes in 12 populations of *Dyckia brevifolia* Baker, Itajaí-Açu River (SC).

Populations		Diametric classes (cm)							Total	Pearson's correlation <i>r</i>
		5-10	10-15	15-20	20-25	25-30	30-35	35-40		
Ressacada	N	-	39	45	17	8	-	-	109	0.98*
	%	-	<b>25.2</b>	<b>40.2</b>	<b>65.4</b>	<b>88.9</b>	-	-	<b>17.8</b>	<i>p</i> = 0.001
Subida/Apiúna I	N	3	82	266	380	194	39	9	973	0.98*
	%	<b>0.4</b>	<b>6.3</b>	<b>20.8</b>	<b>44.5</b>	<b>52.9</b>	<b>76.5</b>	<b>81.8</b>	<b>20.0</b>	<i>p</i> = 0.000
Subida/Ibirama I	N	12	263	448	232	39	5	1	1,000	0.98*
	%	<b>0.6</b>	<b>11.2</b>	<b>32.0</b>	<b>47.4</b>	<b>53.4</b>	<b>71.4</b>	<b>100</b>	<b>13.9</b>	<i>p</i> = 0.000
Subida/Apiúna II	N	-	-	25	69	195	140	41	470	0.93*
	%	-	-	<b>8.7</b>	<b>19.8</b>	<b>58.7</b>	<b>84.8</b>	<b>100</b>	<b>20.4</b>	<i>p</i> = 0.001
Subida/Ibirama II	N	-	-	3	11	25	2	-	41	0.94*
	%	-	-	<b>42.9</b>	<b>55.0</b>	<b>62.5</b>	<b>66.7</b>	-	<b>15.0</b>	<i>p</i> = 0.002
Subida/Apiúna III	N	2	64	116	113	41	8	-	344	0.99*
	%	<b>0.2</b>	<b>4.3</b>	<b>11.6</b>	<b>21.9</b>	<b>31.5</b>	<b>40.0</b>	-	<b>6.0</b>	<i>p</i> = 0.000
Morro Santa Cruz	N	-	18	158	368	209	66	12	831	0.96*
	%	-	<b>1.9</b>	<b>14.5</b>	<b>41.2</b>	<b>52.9</b>	<b>71.0</b>	<b>100</b>	<b>17.7</b>	<i>p</i> = 0.000
Ascurra	N	1	13	37	12	2	-	-	65	0.93*
	%	<b>0.6</b>	<b>9.8</b>	<b>33.9</b>	<b>52.2</b>	<b>100</b>	-	-	<b>9.8</b>	<i>p</i> = 0.006
Encano Baixo	N	-	-	2	8	5	3	1	19	0.84*
	%	-	-	<b>1.7</b>	<b>9.6</b>	<b>17.9</b>	<b>60.0</b>	<b>100</b>	<b>4.1</b>	<i>p</i> = 0.009
Encano	N	-	-	1	16	32	20	33	102	0.89*
	%	-	-	<b>1.6</b>	<b>13.7</b>	<b>26.9</b>	<b>36.4</b>	<b>71.7</b>	<b>20.1</b>	<i>p</i> = 0.003
Salto Weissbach I	N	9	42	85	100	41	13	1	291	0.86*
	%	<b>2.1</b>	<b>10.2</b>	<b>15.9</b>	<b>23.7</b>	<b>25.3</b>	<b>43.3</b>	<b>100</b>	<b>10.1</b>	<i>p</i> = 0.006
Salto Weissbach II	N	-	-	7	5	4	-	-	16	0.78
	%	-	-	<b>8.2</b>	<b>10.0</b>	<b>57.1</b>	-	-	<b>7.8</b>	<i>p</i> = 0.069
Total	N	27	491	1,191	1,331	795	295	98	4,261	0.97*
	%	<b>0.4</b>	<b>6.8</b>	<b>19.6</b>	<b>34.7</b>	<b>47.8</b>	<b>68.8</b>	<b>86.7</b>	<b>14.0</b>	<i>p</i> = 0.0001

\*Significant by Pearson's correlation with  $p < 0.01$ .



**Figure 4.** Demographic structure of *Dyckia brevifolia* considering the average number of rosettes in five populations studied (Subida/Apiúna I, Subida/Apiúna II, Subida/Ibirama I, Morro Santa Cruz and Encano), in an average area of  $1,017.6 \pm 874.4$  m<sup>2</sup>, Itajaí-Açu River (SC). \*Seedling mortality has not been quantified.

**Table 6.** Number of offshoots emitted per rosette naturally (N) and after herbivory by capybara (C) in 5 populations of *Dyckia brevifolia*, Itajaí-Açu River (SC).

Number of shoots per rosette	Populations										Total	
	Subida Apiúna I		Subida Ibirama I		Subida Ibirama III		Morro Santa Cruz		Encano		N	C
	N	C	N	C	N	C	N	C	N	C		
1	146	35	74	-	219	3	214	1	29	682	39	
2	15	2	16	-	38	5	36	6	3	108	13	
3	1	-	-	-	3	9	3	6	1	8	15	
4	-	-	-	-	-	10	3	13	-	3	23	
5	-	-	-	-	-	9	-	10	-	-	19	
6	-	-	-	-	-	-	-	6	-	-	6	
7	-	-	-	-	-	-	-	2	-	-	2	
8	-	-	-	-	-	-	-	2	-	-	2	
12	-	-	-	-	-	-	-	1	-	-	1	
20	-	-	-	-	-	-	-	1	-	-	1	
Total	162	37	90	-	260	36	256	48	33	-	801	121

**Figure 5.** Clonal propagation in *Dyckia brevifolia* Baker, Itajaí-Açu River (SC). (a) Basal clonal emission; (b) Axillary clonal emission; (c) Sprouting after herbivory of *Hydrochaeris hydrochaeris* (capybara).

Regarding axillary emission, each rosette emitted from one to four shoots in the center of the mother-plant (Table 6), and the majority (85.1%) issued only one shoot (Figure 5). It was also found that *D. brevifolia* has herbivory by *Hydrochaeris hydrochaeris* Linnaeus, 1766 (capybara), which mainly consumes the central part of its rosettes (Figure 5). Some populations have more rosettes herbivorated by capybaras. On the other hand, herbivory was not recorded in some populations of *D. brevifolia*. Rosettes consumed by capybara die or often regrow, emitting from one (majority 32%) to 20 shoots (Table 6).

## 4. Discussion

### 4.1. Habitat and occurrence of *D. brevifolia*

The species occurred on the rocky shores or even within the larger bed, however, in areas of low fluvimetric recurrence, being the populations partially or totally submerged during floods. In these sites, the fluvial flow presented high turbulence, which results from the

interdependence of three factors: high altimetric gradients along the canal, rocky bed and higher flow velocities. It should be taken into account that turbulent regimes are conditioned variations in channel depth and flow speed (Bigarella, 2003) and that it is controlled by the hydraulic gradient, the roughness of the bed and the depth of the canal (Summerfield, 1991; Suguio, 2003).

The rosettes of *D. brevifolia* settled on the rock disjunctions (fractures, failures and decompression displacements), present in the two lithotypes (gneisses and rhyolites). These disjunctions possibly facilitate the fixation of individuals and provide better conditions for survival, as they retain organic matter and moisture. In addition, the expansion of the clumps also seemed to occur in the sense of them. Plants can present directional growth, which can admit habitat selection, through their limited mobility within the environment (Salzman, 1985; Bazzaz, 1991). The first evidence of habitat selection, through directional growth, was obtained for bromeliad *Aechmea nudicaulis* in a restinga environment (Sampaio et al., 2004).



As observed, the presence of faults/fractures or displacement in the rocks become abiotic regents important for the nucleation of the species. In addition, it was observed that in these sites it is common to the presence of mosses. The bromeliad *D. maritima* Baker occurs in rocky outcrops and also begins its development on mosses (*Campylopus* spp.) (Waldemar and Irgang, 2003).

It was also observed that seedlings occur clumped, in places with substrate accumulation and presence of moisture, which suggests that each group is composed of more than one genet. According to Benzing (1980), even the most xeric bromeliads, such as species of the genus *Dyckia*, require moisture for germination and the beginning of development. For most bromeliads, aridity and low levels of nutrient availability represent the primary stresses in all life history stages (Hernández et al., 1999; Benzing, 2000). In epiphyte bromeliads, during the early stages of its development, drought is considered the main cause of death (Benzing, 1981; Mondragón et al., 2004; Zotz et al., 2005).

#### 4.2. Demographic structure and sexual and asexual reproduction of *D. brevifolia*

Regarding the demographic structure, the diameter of the rosettes provides an idea of the age of each individual. However, individuals from clonal propagation have faster growth and require less time to become reproductive (Benzing and Davidson, 1979; Ticktin et al., 2003; Mondragón et al., 2004; Rogalski et al., 2021). Seeds of *D. brevifolia*, collected in the study area, after germination in a greenhouse took about seven years to reach reproduction (J. M. Rogalski, personal observation).

The variation in the size of the rosettes of the species probably also occurs due to the light intensity and nutrient availability. In this study, it was found that rosettes in full sun were smaller (diameter of rosettes) than those under the 'sarandis' (shrubs of thin and flexible stems of the banks of rivers) (J. M. Rogalski, personal observation). According Barberis et al. (2020) 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.

According to Abrahamson (1980), the balance between sexual reproduction and clonal propagation has a great influence on population demographics. The populations that presented few rosettes in the initial classes are probably constituted by few individuals generated sexually, and clonal propagation is the main form of recruitment. On the other hand, in the other populations the two forms (sexual and clonal) seem to have importance in the constitution of populations. However, the survey was conducted in a single moment and the populations could present variations over the years.

Although the species presents annual flowering, germination, recruitment (seedlings and offshoots) and mortality rates could vary over the years. Thus, these variations could explain the differences found between the populations evaluated. According to Mondragón et al. (2004), long-term studies are needed to adequately describe the demographics of long-life species, as populations may vary over the years.

The average number of seedlings (164) can be considered low when compared to the average number of reproductive rosettes (675) (Figure 4) and the average number of seeds produced by inflorescence (7,555.7 seeds, with 96% germination in greenhouse; Rogalski et al., 2009). Nevertheless, seedling mortality was not quantified and probably few seedlings were recruited to the populations. In *Vriesea flammea* L.B.Sm. the *in vitro* germination rates above 80% were recorded (Sasamori et al., 2020).

In Encano Baixo and Salto Waissbach II populations no seedlings were recorded. In addition, these populations presented the lowest percentages of reproductive rosettes, which could indicate recent (re)colonization. None seedling was registered for the congener rheophyte *D. ibiramensis* in four populations studied during one year (Rogalski et al., 2021). Studies with bromeliads indicate that individuals produced sexually are more vulnerable (Cogliatti-Carvalho and Rocha, 2001; Villegas, 2001; Mondragón et al., 2004), that the mortality is higher in the initial stages of development and that seedling survival increases with increasing plant size (Augsburger, 1985; Benzing, 2000; Mondragón et al., 2004; Winkler et al., 2005). According to Barberis et al. (2020), in *Aechmea distichantha* Lem. ramet survival was slightly higher for younger, and lower for reproductive ramets.

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 *D. brevifolia*, the larger the diameter of the rosettes, the greater the probability of becoming reproductive. In other studies, with bromeliad species, 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 and Reis, 2009; Filippin et al., 2012; Rogalski et al., 2021).

For successful sexual reproduction, *D. brevifolia* seeds need to reach favorable microhabitats (rocky disjunctions) to germination and seedling development, since the species occurs in an environment that presents nutrient and moisture scarcity (exposed rock). Floods are also an impact factor, as individuals can be carried. Therefore, germination and seedling survival can be considered the main 'bottlenecks' in the life cycle of this species.

In the Bromeliaceae family, in some species like *Puya dasylirioides* (Augsburger, 1985), *Tillandsia deppeana* (García-Franco, 1990), *Aechmea nudicaulis* (Zaluar and Scarano, 2000; Sampaio et al., 2004) and *Aechmea magdalenae* (Villegas, 2001) seedling recruitment rarely occurred or do not occur as in *Dyckia ibiramensis* (Rogalski et al., 2021); while in others, like *Neoregelia johannis* (Cogliatti-Carvalho and Rocha, 2001), *Tillandsia brachycaulos* (Mondragón et al., 2004) and *Werauhia sanguinolenta* (Zotz et al., 2005) the recruitment was frequently observed.

The average number of offshoots emitted was 266 (6% of the total number of rosettes) (Figure 4) and the offshoots are probably less susceptible to environmental stress, as they remain linked to the mother plant,

possibly constituting herbivory by capybaras, in addition to senescence, the main cause of death. Resource sharing between ramets is considered a particular advantage when resources are distributed in discrete locations within the habitat (Cook, 1983), as occurs in this environment.

As the species presents vegetative propagation, the clumps must be composed mainly of offshoots. Considering all the sites evaluated, 97.6% of the rosettes occurred clumped, and most clumps contained up to 10 rosettes. Very similar results were found for the rheophytes *D. ibiramensis* Reitz (Rogalski et al., 2021) and *D. distachya* Hassler (J.M. Rogalski et al., unpublished data). On the other hand, larger clumps may consist of the fusion of smaller clumps when they expand, due to the proximity between them, or they could indicate older clumps. Rheophytes are characterized by having particular morphological characters such as narrow lanceolate leaves or leaflets (stenophyll); matted root systems; short erect, ascending, or creeping rhizomes tightly attached to streambed substrates; and flexible stems and petioles (Imaichi and Kato, 1997).

Clonal propagation makes it difficult to determine the number of genets present in populations. However, the high percentage of clumped rosettes and the number of axillary offshoots emitted indicate that clonal propagation predominates in this species. These results corroborate Harper's conclusions (Harper, 1977), in his review on the dynamics of perennial herbaceous populations, where it is suggested that seed recruitment contributes little to the maintenance of populations.

On the other hand, in addition to seedlings (1,789), isolated rosettes (722) and clumps (2,254) could be considered genets. Rosettes belonging to different clumps were genetically evaluated and some showed different multilocus genotypes, indicating that they are not clones (Rogalski et al., 2017).

Clonal emission in *D. brevifolia* occurred in plants with varied diameter and independent of sexual reproduction. In bromeliads clonal propagation is not restricted to adults and not all reproductive adults produce offshoots (Benzing, 1980). Herbivory apparently stimulated the emission of a greater number of offshoots, as rosettes without herbivory had up to four offshoots, while rosettes with herbivory had up to 20 offshoots.

Clonal propagation can be extremely important for *D. brevifolia*, considering that the species occurs in an environment with adverse conditions (exposed rock, current, dry and flood periods), both for the colonization, due to the founding effect (rapidly increasing the size of populations), and for the maintenance of their populations. In environments that suffer some kind of disturbance species that reproduce asexually are more likely to survive (Janzen, 1980; Cook, 1983). In addition, clonal propagation reduces the risk of genet mortality, as it dilutes the risk among ramets (Cook, 1979), which can help minimize the effects of inbreeding [since the species is self-compatible and autogamy, see Rogalski et al. (2009) and genetic drift throughout generations, as it maintains existing genetic diversity. On the other hand, sexual reproduction can generate genetic diversity (genets).

The reproductive rosettes of *D. brevifolia* were concentrated in the classes with larger diameter

(Rogalski and Reis, 2009), which also occurred in the rheophyte congeners *D. ibiramensis* (Rogalski et al., 2021) and *D. distachya* (J.M. Rogalski et al., unpublished data) and in other bromeliads (Benzing, 1981; Hietz et al., 2002; Mondragón et al., 2004; Duarte et al., 2007; Filippon et al., 2012; Lenzi and Paggi, 2020). Unlike most bromeliads with monocarpic ramets, which die after reproduction (Benzing, 1980; Benzing, 2000), *D. brevifolia* is polycarpic. The longevity of rosettes and clonal propagation seem to be fundamental for the maintenance of the species' populations, since apparently few individuals are recruited sexually.

The structure of plant populations results from the action of biotic and abiotic factors on their current and ancestral members, which affect the spatial arrangement and the age and genetic structures of its components (Hutchings, 1997). In the studied sites, the species was characterized by having few isolated rosettes, by forming small clumps and by the great variation in relation to the number and density, as well as in the distribution of rosettes in diametric classes.

In addition to these factors, the form of recruitment (via sexual reproduction and/or vegetative propagation) in populations seems to be determinant for the demographic structure of *D. brevifolia*. These variations in rosette diameter and in the stages of life (seedling, immature and reproductive rosettes) occur as a function of the (re) colonization time of each of these sites, the characteristics of the rocky substrate (presence of fractures, faults and displacements) and the available area in each site. Thus, long-term studies could help to better understand the differences found between the populations studied.

#### 4.3. Conservation of the rheophyte *D. brevifolia*

With the installation of the Salto Pilão hydroelectric power station, part of the populations of *D. brevifolia* in the municipality of Lontras already were affected by the lake of the dam. The rheophyte *D. brevifolia* showed restricted distribution and occurred in places with specific characteristics (fast, exposed rocks without sediment deposits), which makes its disjunctive distribution along the Itajaí-Açu River. Due to the correlation between the area of occupation of the species and the number of rosettes, the reduction of these microhabitats, mainly by the construction of hydroelectric power plants, implies a practically proportional reduction of this species. Thus, the high environmental specificity presented by *D. brevifolia* makes it very vulnerable to habitat loss and environmental changes.

In addition, the record of a low number of populations, with a predominance of clumps and vegetative propagation, possibly indicates a low number of genets per population. Furthermore, results indicating that much of the genetic diversity of *D. brevifolia* is distributed among its populations (Rogalski et al., 2017).

Our results suggest that the maintenance of sites with these characteristics becomes essential for their long-term conservation. This study with *D. brevifolia* shows the importance of evaluating the biological group rheophytes before the concession of hydroelectric power stations.

Furthermore, understanding the distribution within populations can contribute to the re-introduction and *ex situ* conservation of *D. brevifolia*.

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