

RAMET DEMOGRAPHY OF A NURSE BROMELIAD IN BRAZILIAN RESTINGAS¹

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Restingas are sandy coastal plains that stand between the sea and the Brazilian Atlantic forest mountains. The predominant restinga vegetation type in northern Rio de Janeiro, Brazil, is characterized by the formation of islands that begins with colonization by some pioneer herbs and/or woody plants. Pioneer plants are stress-resistant and nurse many other less-resistant plant species. Determining the spatiotemporal variation in the dynamics of nurse plants is essential to understand the ecological functioning of restingas as a whole. The goal of this study was to analyze the spatiotemporal variation in population dynamics of the nurse bromeliad *Aechmea nudicaulis*. We monitored *A. nudicaulis* ramets in different habitats, microhabitats, and years. We analyzed the spatiotemporal variation in demographic traits and in population growth rate. Results showed young ramet traits were more variable at the microhabitat level, and when variable, vegetative ramet traits varied at all spatiotemporal scales. Overall, λ values indicated that *A. nudicaulis* basically remained spatiotemporally stable as most of the λ values did not significantly differ from unity. Hence, the stability of *A. nudicaulis* in different microhabitats and habitats in the restinga may create several settlement opportunities for many other less-resistant species.

Key words: *Aechmea nudicaulis*; Brazil; Bromeliaceae; life-cycle traits; nurse plants; population dynamics; restinga.

The Brazilian Atlantic rainforest is considered one of the 25 biodiversity hotspots containing high species diversity and high levels of endemism (Fonseca, 1985; Myers et al., 2000). The Atlantic coastal vegetation of Brazil comprises several plant communities, such as different forest types (e.g., coastal and montane rainforests and semi-deciduous forests) and open vegetation (Scarano, 2002). Plant communities at the periphery of the Atlantic rainforest (e.g., swamp forests, restingas, and high altitude fields) are subjected to more extreme environmental conditions than plants in the mesic rainforest, mainly due to drought, salinity, and/or nutrient deficiency (Scarano et al., 2001). Restingas are sandy coastal plains formed by a mosaic of plant communities interspersed with beach ridges and lagoon systems that stand between the sea and the Atlantic forest mountain chain (Lacerda et al., 1993; Scarano, 2002). The most characteristic vegetation type of the restingas is structured by the formation of islands, and succession is triggered by the ability to colonize bare sand by some pioneer herbs and/or woody plants. In northern Rio de Janeiro, southeastern Brazil, one of the most thoroughly studied restingas in the country, the establishment of small vegetation islands is driven by some palms [e.g., *Allagoptera arenaria* (Gomes) Kuntze], bromeliads [e.g., *Aechmea nudicaulis* (L.) Griseb.], and some woody plants (e.g., *Clusia hilariana* Schlecht.) that act as nurse plants favoring the entry of many other plant species (Zaluar and Scarano, 2000; Scarano, 2002). Nurse plants provide shelter from high temperatures that make seedling establishment rare for plant species less resistant to harsh conditions (Flores and Jurado, 2003).

Interestingly, nurse plants in restingas are often terrestrial

forms of typical epiphytes of the neighboring Atlantic rainforest (Scarano, 2002). Moreover, most nurse plants in restingas exhibit crassulacean acid metabolism, such as some bromeliads and particularly some species of the genus *Clusia* (Reinert et al., 1997; Lüttge, 1999; Scarano, 2002). This mode of photosynthesis acts as a stress-resistant mechanism maximizing water-use efficiency. Hence, it has been hypothesized that stress-resistant plants from the Atlantic rainforest have migrated to the geologically younger lowlands where they nurse seeds and seedlings of other less-resistant plant species. The exchange of plant species between contrasting habitats (e.g., from rocky habitats to the canopy of neighboring forests and from the canopy of rainforests to restingas) may have been a common process in the Brazilian Atlantic rainforest complex, particularly prior to the current levels of fragmentation. This process has been considered one of the factors accounting for the high plant diversity found in these rainforests (Scarano, 2002). The extent of the exchange is large since approximately 80% of the plant species occurring in restingas of the state of Rio de Janeiro are also found in montane rainforests (Araujo, 2000). The ability of some plant species to colonize marginal habitats where they nurse other plant species may be of key relevance in a global change scenario, because it suggests high levels of plant morpho-physiological and ecological plasticity to distinct environmental conditions (Scarano, 2002).

Determining the spatiotemporal variation in dynamics of nurse plants is essential to understanding the ecological functioning of restingas (Zaluar and Scarano, 2000; Liebig et al., 2001; Scarano, 2002). Given that restingas are a mosaic of plant communities and environments, the establishment probabilities of nurse plants, and therefore of the other plants that depend on nurse plants, may greatly differ depending on the effects of spatial and temporal heterogeneity on their performance. The goal of this study was to determine the spatiotemporal variation in demographic attributes (i.e., survival, growth, and reproduction) and population dynamics of the nurse plant *Aechmea nudicaulis*. To our knowledge, this is one of the first studies examining the detailed demography of a

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plant species occurring in Brazilian restingas (but see Cirne and Scarano, 2001). The bromeliad *A. nudicaulis* is a clonal plant with a vigorous vegetative reproduction that allows a single fragment to potentially occupy a large area, forming large ramet systems (Sampaio et al., 2002). It has been shown that germination of *Clusia hilariana*, the main nurse tree in this vegetation (Zaluar and Scarano, 2000; Liebig et al., 2001), takes place predominantly inside the tanks formed by this bromeliad (Scarano, 2002). However, no aspects related to the growth dynamics of *A. nudicaulis* are known to date, including flowering phenology and age. We selected three different habitats within a restinga in northern Rio de Janeiro state, Brazil, differing in the distance to the coastline and vegetation cover. Within each habitat, we defined four different microhabitats (from bare sand to mature vegetation islands) where *A. nudicaulis* can be found. We analyzed the spatial (among habitats and microhabitats) and temporal (across years) variation in all demographic traits of this clonal bromeliad in order to build projection matrices to estimate the spatiotemporal variation in dynamics of *A. nudicaulis* populations.

MATERIALS AND METHODS

Plant species and study site—*Aechmea nudicaulis* is a terrestrial, clonal-tank bromeliad (60–90 cm height) widely distributed across Central and South America (Smith and Downs, 1979). Ramets form tanks that harvest water and litter and usually house animals such as frogs and lizards. Like many other species of the Bromeliaceae family, *A. nudicaulis* exhibits a semelparous life cycle (Sampaio et al., 2002). Ramets produce 1–2 new ramets per year, and the distance between ramets is approximately 10 cm. Rhizomes are usually buried at 5 cm in the soil and last longer than the ramets. After the death of the ramet, an underground vestige can be found, indicating the previous existence of a ramet (Sampaio et al., 2002). Flowering mainly takes place between May and October. Inflorescences (60–100 cm height) are upright panicles and include several yellow flowers.

This study was conducted at Restinga de Jurubatiba National Park (22°23' S, 41°45' W; 14 140 ha), RJNP hereafter. Climate at RJNP is tropical and markedly seasonal with mean minimum temperature of 20°C, mean maximum temperature of 30°C, and annual rainfall of 1164 mm concentrated in summer (November to February). The two study years were similar in regard to rainfall (ca. 1000 mm) and climate as a whole (data from the local climate station). A comprehensive description of vegetation types and main plant species occurring in Brazilian restingas can be found in Lacerda et al. (1993).

Population sampling—No seedlings were observed for *A. nudicaulis* during the period of study. In fact, sexual recruitment seems to be a rare event among many restinga plant species (e.g., Cirne and Scarano, 2001), especially in the case of *A. nudicaulis* (Sampaio et al., 2002). Demographic data were totally obtained from *A. nudicaulis* clonal fragments located in three habitat types and four microhabitats within each habitat monitored from 2001 to 2003. All fragments within each microhabitat in each habitat were considered as a population. Habitats were beach ridges that differed in their distance from the sea (near, intermediate, and far) and in vegetation cover (low, intermediate, and high). The three habitats were located at approximately 100, 500, and 600 m from the coastline and had low (20%), intermediate (29%), and high (42%) vegetation cover, respectively. Vegetation cover was estimated by Pimentel (2002) by using line intercepts and measuring the proportional length of the projected vegetation cover vs. open areas upon each of them. The distance between habitats ranged about 1000–2000 m. Four microhabitats were identified within each habitat where *A. nudicaulis* occurred: (1) bare sand, (2) associated with the palm *Allagoptera arenaria*, (3) neighboring zones at the border of vegetation islands, and (4) shaded zones inside vegetation islands. A total of two plots (100 × 100 m) were laid down within each habitat including all four microhabitats. A total of 96 *A. nudicaulis* fragments occurring in the four microhabitats were monitored within each habitat

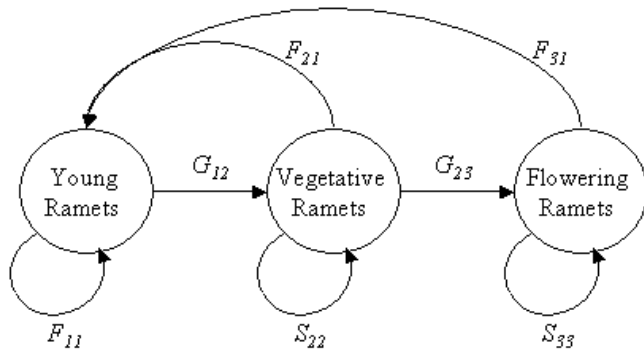
TABLE 1. Number of fragments and ramets of *Aechmea nudicaulis* populations in different habitats (low, intermediate, and high vegetation cover) and microhabitats (bare sand, palm, at the border and inside vegetation islands) in the first year of study. The number of fragments did not change, and there was little variation in the number of ramets between the years of study.

Microhabitat	Low cover		Intermediate cover		High cover	
	Fragments	Ramets	Fragments	Ramets	Fragments	Ramets
Bare sand	47	135	43	124	28	82
Palm	14	73	21	65	18	49
Border	25	149	23	84	36	202
Inside	10	56	9	45	14	85

(overall 288 fragments; see Table 1). The number of live ramets per fragment remained fairly constant between habitats, microhabitats, and years, and a total of 1149, 1116, and 1173 ramets were tagged and monitored in 2001, 2002, and 2003, respectively. Censuses were conducted in April/May. Given that we could not determine whether different fragments also corresponded to different genets, we used individual ramets as demographic units. Ramet demography of *A. nudicaulis* was therefore determined by pooling all ramets from all fragments of each microhabitat within each habitat, and monitoring their demographic attributes over time. At each census, height (the variable that best represents the growth of *A. nudicaulis*; Sampaio et al., 2002), status (vegetative/reproductive), and fate (dead/alive) of each ramet were recorded. New ramets produced by extant ramets were also tagged and measured. Ramets always remained connected to their mother plants. These basic data were used to build population projection matrices for 2 yr (from 2001–2002 to 2002–2003) for each microhabitat within each habitat. No seedlings were observed during the two years of study. Although we did not conduct germination experiments in the field, Pinheiro and Borghetti (2003) carried out laboratory experiments for seed germination and verified that the germination rate of *A. nudicaulis* seeds is very high (>90%), but seeds are very sensitive to heat and drought. Pinheiro and Borghetti (2003) showed that seeds did not germinate after being exposed to 50°C, and 4 d of imbibition were necessary to germinate. Given that in restingas the temperature at the sand surface in summer can reach up to 70°C at the peak of the radiation (Scarano, 2002), *A. nudicaulis* seed germination in natural conditions may only take place in very specific and infrequent conditions and seed banks are not formed.

Demographic model—Population projection matrices were of the Lefkovich type in which classification of plants is based on size or developmental stage (Caswell, 2001). The projection matrix model used had the form: $n(t+1) = \mathbf{A}n(t)$, where $n(t)$ and $n(t+1)$ are vectors whose elements, a_i , are the number of individuals that belong to the i th category at time t and $t+1$, respectively. \mathbf{A} is the population projection matrix, whose elements, a_{ij} , represent the transitions or contributions from individuals in the j th category to the i th category over one time step. The dominant eigenvalue λ of the matrix gives the population growth rate. The associated right and left eigenvectors \mathbf{w} and \mathbf{v} give the stable-stage distribution and the reproductive values of each stage class, respectively (Caswell, 2001).

The life-cycle graph and its corresponding population projection matrix for *A. nudicaulis* had three stages: young ramets, vegetative ramets, and reproductive ramets (Fig. 1). Vegetative ramets were easily differentiated from reproductive ramets that produced inflorescences and generally died after flowering. Young ramets were differentiated from vegetative ramets using two biological criteria: (1) young ramet height was set below 36 cm, which was the average height of 1-yr-old ramets, and (2) flowering probabilities of ramets below 36 cm were nil. Vegetative ramets were all classified in one category because once a ramet reaches the vegetative stage its growth rate turns out to be very low so that size differences between years are very small. Using these criteria, all ramets were classified into their corresponding size/stage categories, and their fate (i.e., stasis, change of category or death) was also recorded from one year to another. As a result, we built 24 matrices (2 yr × 3 habitats × 4 microhabitats).



		Stage at time <i>t</i>		
		Young	Vegetative	Flowering
Stage at time <i>t</i> + 1	Young	F_{11}	F_{21}	F_{31}
	Vegetative	G_{12}	S_{22}	0
	Flowering	0	G_{23}	S_{33}

Fig. 1. Life cycle graph of *Aechmea nudicaulis* and its corresponding population projection matrix. Circles correspond to stages, while arrows correspond to transitions. The first row of the matrix indicates the production of new ramets by each class (F_{ij}), the diagonal indicates the survival of vegetative and flowering in the same class (S_{ij}), and the subdiagonal indicates the growth to larger classes (G_{ij}).

Data treatment and matrix analyses—The effects of year, habitat, and microhabitat on the probability of ramet production by young and vegetative ramets were tested with logistic regression models. The analysis started with a null model including all main factors (year, habitat, and microhabitat) and all interactions. Then, a new model that lacked the factor to be analyzed was created. Subsequently, for each factor we tested whether the difference in unexplained variance between models was approximately χ^2 distributed, with the number of degrees of freedom equal to the difference between models (Caswell, 2001). The probability of ramet production by flowering ramets was very low and was not analyzed.

The effects of year, habitat, and microhabitat on the fate of young (growth to vegetative or death) and vegetative (survival, growth to flowering or death) ramets were tested with log linear analyses. The analysis started with the null model YHM, F, which indicates that year (Y), habitat (H), and microhabitat (M) had an independent effect on fate (F). New models were created to test the effect of each factor on fate. The difference between each new model and the null model gave the unexplained variance between models that is χ^2 distributed, with the number of degrees of freedom equal to the difference between models (Caswell, 2001).

We used Monte Carlo simulations to generate confidence intervals for population growth rate, λ , according to the method developed by Alvarez-Buylla and Slatkin (1993). The method basically assumes that estimated demographic parameters are the sum of the actual value plus an error term that represents the error made in estimating demographic parameters. In order to include the error term in the simulations, the method takes into account the observed variance estimates for ramet production, whereas the sampling variances for transition probabilities were estimated according to a binomial distribution. Variability in ramet production was also sampled from a binomial distribution because *A. nudicaulis* ramets only produced a range of 0–3 new ramets a year. The method also accounts for the effects of truncating the distribution of matrix errors so that only biologically possible values occur. For each one of the 24 observed matrices, we conducted 100 simulations obtaining 100 new simulated matrices. As a result, 100 new population growth rates were produced from which the standard error (σ) was used to calculate approximate 95% confidence intervals (i.e., $\lambda \pm 2\sigma$).

Elasticity analyses were performed on projection matrices of each site to determine the relative contribution of demographic traits to population growth rate, λ (Caswell, 2001). The sensitivity of λ to a change in the matrix entry a_{ij} ($s_{ij} = \partial\lambda/\partial a_{ij}$) measures how changes in individual demographic parameters influence λ . The elasticity ($e_{ij} = s_{ij} \times a_{ij}/\lambda$) of λ to a change in a_{ij} is a measure of proportional sensitivity and quantifies the proportional change in λ resulting from a proportional change in a_{ij} (Caswell, 2001). The routine to compute confidence intervals as well as population growth rates, sensitivities, and elasticities were all generated with MATLAB (MathWorks, 1997).

RESULTS

The life cycle of *A. nudicaulis* was characterized by the fairly high survival rates of young and vegetative ramets (Table 2). Young ramets exhibited high growth rates at the veg-

TABLE 2. Mean (± 1 SE) population projection matrices of *Aechmea nudicaulis* populations in different habitats (low, intermediate, and high vegetation cover) and microhabitats (bare sand, palm, at the border and inside vegetation islands). The variance corresponds to the variability in matrix entries between the two years of study. Classes: YR, young ramets; VR, vegetative ramets; FR, flowering ramets. Nonexistent matrix entries are indicated by dashes.

	Low cover			Intermediate cover			High cover		
	YR	VR	FR	YR	VR	FR	YR	VR	FR
Bare sand									
YR	0.32 \pm 0.14	0.35 \pm 0.03	—	0.37 \pm 0.09	0.24 \pm 0.06	0.04 \pm 0.05	0.50 \pm 0.37	0.23 \pm 0.00	0.20 \pm 0.28
VR	0.92 \pm 0.03	0.56 \pm 0.08	—	0.89 \pm 0.00	0.53 \pm 0.13	—	0.89 \pm 0.10	0.54 \pm 0.15	—
FR	—	0.11 \pm 0.01	0.08 \pm 0.12	—	0.20 \pm 0.05	0.19 \pm 0.27	—	0.12 \pm 0.05	0.20 \pm 0.28
Palm									
YR	0.52 \pm 0.07	0.26 \pm 0.00	0.20 \pm 0.28	0.45 \pm 0.01	0.22 \pm 0.04	0.25 \pm 0.35	0.24 \pm 0.01	0.36 \pm 0.12	0.17 \pm 0.24
VR	0.97 \pm 0.04	0.60 \pm 0.01	—	0.97 \pm 0.04	0.59 \pm 0.02	—	0.85 \pm 0.14	0.66 \pm 0.08	—
FR	—	0.14 \pm 0.02	0.10 \pm 0.14	—	0.07 \pm 0.01	0.00 \pm 0.00	—	0.02 \pm 0.02	0.00 \pm 0.00
Border									
YR	0.59 \pm 0.00	0.31 \pm 0.05	0.08 \pm 0.12	0.50 \pm 0.00	0.30 \pm 0.03	0.10 \pm 0.14	0.39 \pm 0.02	0.27 \pm 0.03	—
VR	0.86 \pm 0.00	0.60 \pm 0.03	—	0.97 \pm 0.04	0.58 \pm 0.01	—	0.85 \pm 0.06	0.63 \pm 0.03	—
FR	—	0.15 \pm 0.07	0.50 \pm 0.00	—	0.11 \pm 0.07	0.30 \pm 0.42	—	0.10 \pm 0.03	0.36 \pm 0.31
Inside									
YR	0.89 \pm 0.44	0.37 \pm 0.06	—	0.25 \pm 0.18	0.30 \pm 0.03	—	0.53 \pm 0.31	0.20 \pm 0.05	—
VR	0.83 \pm 0.24	0.58 \pm 0.05	—	0.78 \pm 0.13	0.57 \pm 0.01	—	0.95 \pm 0.07	0.64 \pm 0.00	—
FR	—	0.11 \pm 0.12	0.55 \pm 0.07	—	0.10 \pm 0.09	0.17 \pm 0.24	—	0.03 \pm 0.04	0.37 \pm 0.05

TABLE 3. Mean (± 1 SE) elasticity values (%) of *Aechmea nudicaulis* populations in different habitats (low, intermediate, and high vegetation cover) and microhabitats (bare sand, palm, at the border and inside vegetation islands). The variance corresponds to the variability in elasticity values between the two years of study. Classes: YR, young ramets; VR, vegetative ramets; FR, flowering ramets. Nonexistent matrix entries are indicated by dashes.

	Low cover			Intermediate cover			High cover		
	YR	VR	FR	YR	VR	FR	YR	VR	FR
Bare sand									
YR	12.31 \pm 5.0	27.34 \pm 3.3	—	16.64 \pm 8.7	23.00 \pm 5.4	1.14 \pm 1.6	23.18 \pm 16.2	21.96 \pm 8.6	1.48 \pm 2.1
VR	27.34 \pm 3.3	33.01 \pm 1.6	—	24.14 \pm 3.8	33.14 \pm 13.6	—	23.44 \pm 6.5	27.21 \pm 6.2	—
FR	—	0.00 \pm 0.0	0.00 \pm 0.0	—	1.14 \pm 1.6	0.80 \pm 1.1	—	1.48 \pm 2.1	0.76 \pm 1.1
Palm									
YR	21.64 \pm 5.6	20.87 \pm 3.5	2.53 \pm 3.6	18.61 \pm 0.1	21.37 \pm 0.4	1.67 \pm 2.4	7.47 \pm 1.4	24.44 \pm 3.1	0.00 \pm 0.0
VR	23.40 \pm 0.1	28.46 \pm 1.05	—	23.04 \pm 1.9	33.63 \pm 6.3	—	24.44 \pm 3.1	43.65 \pm 7.6	—
FR	—	2.53 \pm 3.6	0.56 \pm 0.8	—	1.67 \pm 2.4	0.00 \pm 0.0	—	0.00 \pm 0.0	0.00 \pm 0.0
Border									
YR	24.81 \pm 1.2	21.56 \pm 1.1	1.50 \pm 2.1	20.05 \pm 1.7	22.43 \pm 4.6	2.06 \pm 2.9	14.55 \pm 0.4	23.03 \pm 0.9	—
VR	23.06 \pm 1.1	26.45 \pm 4.5	—	24.48 \pm 1.7	26.55 \pm 1.1	—	23.03 \pm 0.9	39.39 \pm 1.4	—
FR	—	1.50 \pm 2.1	1.12 \pm 1.6	—	2.06 \pm 2.9	2.38 \pm 3.4	—	0.00 \pm 0.0	0.00 \pm 0.0
Inside									
YR	31.70 \pm 3.1	23.04 \pm 0.6	—	10.18 \pm 8.5	24.87 \pm 1.1	—	23.09 \pm 17.4	20.11 \pm 0.5	—
VR	23.04 \pm 0.6	22.21 \pm 4.3	—	24.87 \pm 1.1	40.07 \pm 6.3	—	20.11 \pm 0.5	36.69 \pm 18.4	—
FR	—	0.00 \pm 0.0	0.00 \pm 0.0	—	0.00 \pm 0.0	0.00 \pm 0.0	—	0.00 \pm 0.0	0.00 \pm 0.00

TABLE 4. Logistic regressions testing the effects of year (2001–2002 and 2002–2003), habitat (low, intermediate, and high vegetation cover) and microhabitat (bare sand, palm, at the border and inside vegetation islands) on the probability of ramet production from young ramets and vegetative ramets of *Aechmea nudicaulis*.

Effect	Young ramets		Vegetative ramets	
	df	χ^2	df	χ^2
Year (Y)	1	0.18 ns	1	2.55 ns
Habitat (H)	2	4.06 ns	2	0.35 ns
Microhabitat (M)	3	9.28*	3	1.84 ns
Y \times H	2	0.53 ns	2	3.85 ns
Y \times M	3	4.63 ns	3	5.91 ns
H \times M	6	16.58*	6	3.05 ns
Y \times H \times M	6	5.67 ns	6	7.39 ns

Note: * $P < 0.01$; ns, nonsignificant.

etative stage. Flowering rates were low and ramets presented high mortality rates after flowering. Production of new ramets was low for all stages. Elasticity analyses clearly indicated that the young/vegetative ramet loop accumulated almost all the elasticity of the system and that this pattern was highly consistent between habitats, microhabitats, and years (Table 3).

Young ramets exhibited higher individual ramet production rates (mean ± 1 SE new ramets per young ramet over habitats, microhabitats, and years = 0.46 ± 0.05) than vegetative (0.28 ± 0.01) and flowering ramets (0.09 ± 0.03). New ramet production was more variable among young ramets than among vegetative ramets (Table 4). New ramet production from young ramets significantly varied between microhabitats and the habitat \times microhabitat interaction was also significant (Table 4). In fact, the pattern of new ramet production among microhabitats was different in each habitat (Fig. 2). New ramet production peaked inside vegetation islands in lowly vegetated habitats whereas another peak was observed in bare sand in highly vegetated habitats (Fig. 2). New ramet production from vegetative ramets was not variable at all (Table 4).

Overall, the fate of young ramets was more variable than that of vegetative ramets. The proportion of young ramets becoming vegetative ramets mainly varied between microhabitats and all interactions between microhabitat and the rest of factors were also significant (Table 5). The pattern of variation between microhabitats in the proportion of young ramets becoming vegetative ramets was different for each habitat in

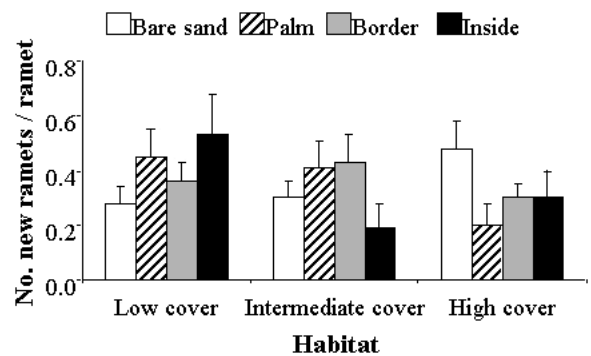


Fig. 2. Mean (± 1 SE) number of new ramets produced by the young ramet class of *Aechmea nudicaulis* in the four microhabitats (bare sand, palm, at the border and inside vegetation islands) within each habitat of study. Means were obtained by pooling ramets from each microhabitat and habitat of the two years of study.

TABLE 5. Loglinear analyses of the effects of year (Y; 2001–2002 and 2002–2003), habitat (H; low, intermediate, and high vegetation cover), microhabitat (M; bare sand, palm, at the border and inside vegetation islands), and fate (F; growth and death for young ramets and survival, growth, and death for vegetative ramets) in *Aechmea nudicaulis*. All models were tested against the YHM, F model (df = 23 and 46, $\chi^2 = 210.70$ and 144.35 for young ramets and vegetative ramets, respectively; see *Data treatment and matrix analyses* in the Materials and Methods). *** $P < 0.001$; ** $P < 0.01$; ns, nonsignificant.

Model	Effect	Young ramets		Vegetative ramets	
		df	χ^2	df	χ^2
YHM, YF	Year (Y)	1	0.00 ns	2	28.11***
YHM, HF	Habitat (H)	2	1.64 ns	4	22.51***
YHM, MF	Microhabitat (M)	3	16.73***	6	22.63***
YHM, YF, HF	Y \times H	3	1.64 ns	6	50.73***
YHM, YF, MF	Y \times M	4	16.74**	8	50.58***
YHM, HF, MF	H \times M	5	18.38**	10	45.31***
YHM, YF, HF, MF	Y \times H \times M	6	18.39**	12	73.63***

each year, and no general patterns of variation were found (Fig. 3). In contrast, the fate of vegetative ramets was even more variable at all spatiotemporal levels of variation (Table 5), also without a clear pattern of variation. The patterns of variation between microhabitats in the proportion of vegetative ramets that remained as vegetative in each year of study and the proportion of vegetative ramets that flowered each year were different for each habitat and year of study (Fig. 4). Nevertheless, the clearest pattern of variation seemed to emerge between years. In general, stasis was lower for ramets in bare sand than in the rest of microhabitats for all habitats in 2001–2002, and growth to flowering tended to be lower in all microhabitats and habitats in 2001–2002 than in 2002–2003, except for ramets in bare sand in all habitats that exhibited the opposite pattern (Fig. 4).

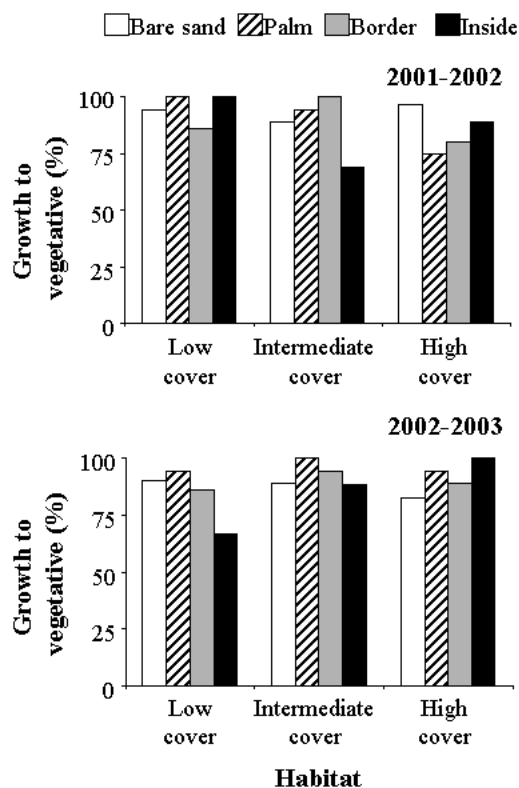


Fig. 3. Percentage of young ramets of *Aechmea nudicaulis* that reached the vegetative class in the four microhabitats (bare sand, palm, at the border and inside vegetation islands) within each habitat and year of study.

Spatiotemporal variation in demographic parameters determined altogether the spatiotemporal variation in population growth rates, λ , of *A. nudicaulis*. Most of the λ values estimated for *A. nudicaulis* (20 of 24) did not significantly differ from unity, i.e., the estimated confidence intervals encompassed unity (Fig. 5), indicating that *A. nudicaulis* populations basically remained stable over time. It must be emphasized, however, that estimated confidence intervals for many populations are quite large as a result of the high variability in demographic attributes within *A. nudicaulis* populations. One of the exceptions where λ significantly differed from unity was found inside vegetation islands in the sparsely vegetated habitat in 2001–2002 (Fig. 5). The other λ values significantly different from unity were observed in the highly vegetated habitat (Fig. 5), indicating that in this habitat the dynamics of *A. nudicaulis* populations were more variable than in the rest of habitats. In highly vegetated habitats, microhabitats in bare

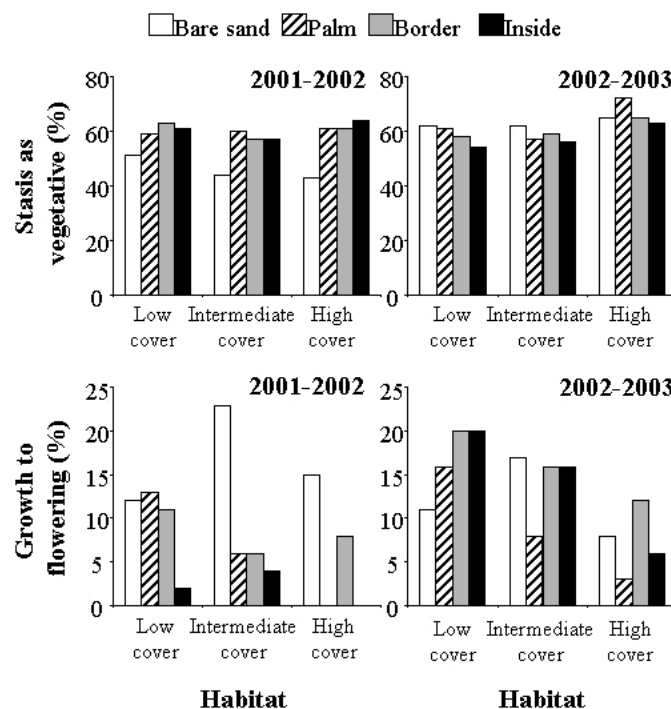


Fig. 4. Percentage of vegetative ramets of *Aechmea nudicaulis* that remained as vegetative or shifted to the flowering class in the four microhabitats (bare sand, palm, at the border and inside vegetation islands) within each habitat and year of study.

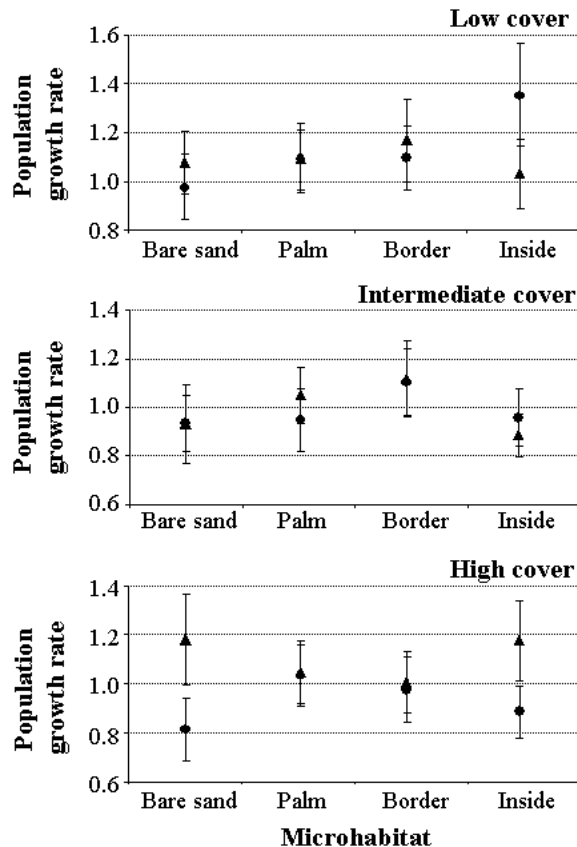


Fig. 5. Population growth rates, λ , with 95% confidence intervals for *Aechmea nudicaulis* populations in the four microhabitats (bare sand, palm, at the border and inside vegetation islands) within each habitat and year of study. Circles correspond to 2001–2002 and triangles to 2002–2003.

sand and inside vegetation islands yielded λ values with the highest temporal variation whereas those in palms and at the border of vegetation islands exhibited low temporal variation (Fig. 5). Moreover, in highly vegetated habitats, λ values from different years in bare sand and inside vegetation islands significantly differed from one another, i.e., one λ did not fall within the confidence interval of the other (Fig. 5). Populations in the habitat with intermediate vegetation cover exhibited the less variable λ values (Fig. 5).

DISCUSSION

Spatiotemporal variation in demographic attributes—We analyzed the spatiotemporal variation in demographic attributes and population dynamics of the nurse plant *Aechmea nudicaulis*. Although this study was based on two years of data (three sampling periods), young ramets differed from vegetative ramets of *A. nudicaulis* in their spatiotemporal pattern of variation. The probability of ramet production from young ramets significantly varied between microhabitats although the pattern of variation between microhabitats also differed between habitats. In contrast, the probability of ramet production from vegetative ramets was totally constant across habitats, microhabitats, and years. Such a difference in the spatiotemporal variation in ramet production between young and vegetative ramets could be attributed to the fact that ramet production tends to be size dependent in clonal plants (Hutchings

and Barkham, 1976; Carlsson and Callaghan, 1990; Wijesinghe and Whigham, 1997; Cirne and Scarano, 2001). Some studies have shown that both the number and size of new ramets increased with ramet size (Wikberg and Svensson, 2003), whereas others have found no relationship between ramet size and probability of ramet production (Bullock, 1980; Chazdon, 1992; Mendoza and Franco, 1998). In the case of *A. nudicaulis*, young ramets produce more new ramets than vegetative and flowering ramets although the probability of ramet production is much more variable for young ramets than for vegetative ramets. In fact, *A. nudicaulis* seems to behave quite differently from other clonal plants that preferentially allocate more resources to developing a storage system and to increasing ramet size during the first stages of the life cycle (De Steven, 1989; Cheplick, 1995; Mendoza and Franco, 1998; Cirne and Scarano, 2001).

On the other hand, ramet fate was more variable across habitats, microhabitats, and years for vegetative ramets than for young ramets. It must be emphasized that, when variable, the fate of young ramets significantly varied between microhabitats and all interactions including microhabitat and the other factors of study were also significant. Hence, for young ramets, microhabitat was the most important source of variation determining the production and fate of new ramets. In general, however, the spatiotemporal pattern of variation in production and fate of ramets was quite difficult to interpret for both young and vegetative ramets. This result suggests that small-scale population characteristics (e.g., below- and aboveground interactions with other plants) ultimately determined the performance of *A. nudicaulis* plants. Other studies on other plant species also indicated that small-scale population characteristics could account for a large proportion of unexplained variance in demographic attributes (Quintana-Ascencio and Menges, 2000; Albert et al., 2001; Riba et al., 2002). Further studies focusing on specific microhabitat characteristics are needed to elucidate the factors affecting performance in *A. nudicaulis* plants. Apart from bare sand, the rest of the microhabitats can be quite heterogeneous, especially the neighboring areas around palms and vegetation islands.

Spatiotemporal variation in population dynamics—Overall, population growth rates, λ , and their estimated confidence interval around unity clearly indicated the high stability of *A. nudicaulis* populations across habitats, microhabitats, and years. Given the fact that λ values were basically determined by ramet fate and ramet production from young and vegetative ramets, the moderate spatiotemporal variation exhibited by these demographic parameters can account for the low variation in λ . There were, however, two exceptions to this pattern. One was the population in sparsely vegetated habitats that peaked inside vegetation islands in one of the years. An extraordinary peak of ramet production from young ramets accounted for that positive λ . The other exception was found in highly vegetated habitats where populations growing in bare sand and inside vegetation islands exhibited significant negative and positive λ values in the same years. Negative and positive λ values were accounted for by low and high ramet production values, respectively, especially from young ramets. Hence, highly vegetated sites were the habitats that produced more spatiotemporal variation in ramet production that in turn affected the dynamics of *A. nudicaulis* populations. It has clearly been demonstrated from theoretical and empirical points of view that increasing variation in demographic traits

leads to increasing extinction probabilities due to a higher temporal variation in λ (Tuljapurkar and Orzack, 1980; Caswell, 2001). Hence, *A. nudicaulis* populations in bare sand and inside vegetation islands in highly vegetated habitats might have higher extinction probabilities than populations next to palms and at the border of vegetation islands. The effect of the vegetation driven by interspecific competition for space (bare sand) or resources (inside islands) might account for this result. However, given the long life span of the species and its vigorous clonal reproduction, *A. nudicaulis* might easily cope with temporal variation in λ as shown by other clonal and long-lived plant species (Eriksson, 1996; Picó and Riba, 2002).

The other demographic trait that characterized the dynamics of *A. nudicaulis* populations is the low impact of flowering ramets on λ , given their low ramet production and high mortality rates. Moreover, no seedlings were observed during the three years of study. Hence, the demographic implications of sexual reproduction of *A. nudicaulis* in restingas is apparently nil over the time period of study. Such a low importance of sexual reproduction has also been observed in other clonal plants (Wikberg and Svensson, 2003). Although sexual reproduction in restingas might be seen as a developmental constraint, flowering *A. nudicaulis* plants might play an important ecological role on a larger spatial and temporal scale. In particular, given the fact that *A. nudicaulis* belongs to the group of plants growing as terrestrials in restingas and as preferential epiphytes in the rainforest, flowering of *A. nudicaulis* in restingas might be seen as a genetic pool that maintains the gene flow between restinga and rainforest populations. However, this is unlikely to occur because the degree of fragmentation is presently very high, as the Brazilian Atlantic rainforest has been reduced to only 7.5% of its original area (Scarano, 2002), and the distance between the restinga and the montane rainforest is also very large (approximately 70 km).

Plant communities marginal to the Atlantic rainforests are structurally and functionally dependent on a small number of nurse plants (Scarano, 2002). Our results suggest that the occurrence of one such plant, *A. nudicaulis*, in different microhabitats within the restinga, where the plant can maintain stable populations, may create a wide array of settlement opportunities for several other plant species less resistant to the rigorous environmental conditions occurring in restingas.

LITERATURE CITED

- ALBERT, M. J., A. ESCUDERO, AND J. M. IRIONDO. 2001. Female reproductive success of narrow endemic *Erodium paularense* in contrasting microhabitats. *Ecology* 82: 1734–1747.
- ALVAREZ-BUYLLA, E. R., AND M. SLATKIN. 1993. Finding confidence limits on population growth rates: Monte Carlo test of a simple analytic method. *Oikos* 68: 273–282.
- ARAÚJO, D. S. D. 2000. Análise florística e fitogeográfica das restingas do Estado do Rio de Janeiro. D.Sc. thesis, Universidade Federal do Rio de Janeiro, Brazil.
- BULLOCK, S. H. 1980. Demography of an undergrowth palm in littoral Cameroon. *Biotropica* 12: 247–255.
- CARLSSON, G. A., AND T. V. CALLAGHAN. 1990. Programmed tiller differentiation, intraclonal density regulation and nutrient dynamics in *Carex bigelowii*. *Oikos* 58: 219–230.
- CASWELL, H. 2001. Matrix population models: construction, analysis, and interpretation, 3rd ed. Sinauer, Sunderland, Massachusetts, USA.
- CHAZDON, R. 1992. Patterns of growth and reproduction of *Geonoma congesta*, a clustered understory palm. *Biotropica* 25: 43–51.
- CHEPLICK, G. P. 1995. Life history trade-offs in *Amphibromus scabrivalvis* (Poaceae): allocation to clonal growth, storage, and cleistogamous reproduction. *American Journal of Botany* 82: 621–629.
- CIRNE, P., AND F. R. SCARANO. 2001. Resprouting and growth dynamics after fire of the clonal shrub *Andira legalis* (Leguminosae) in a sandy coastal plain in southeastern Brazil. *Journal of Ecology* 89: 351–357.
- DE STEVEN, D. 1989. Genet and ramet demography of *Oenocarpus mapora* ssp. *mapora*, a tropical palm of Panamanian tropical moist forest. *Journal of Ecology* 77: 579–596.
- ERIKSSON, O. 1996. Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos* 77: 248–258.
- FLORES, J., AND E. JURADO. 2003. Are nurse-protége interactions more common among plants from arid environments? *Journal of Ecology* 14: 911–916.
- FONSECA, G. A. B. 1985. The vanishing Brazilian Atlantic Forest. *Biological Conservation* 34: 17–43.
- HUTCHINGS, M. J., AND P. B. BARKHAM. 1976. An investigation of shoot interactions in *Mercurialis perennis* L., a rhizomatous perennial herb. *Journal of Ecology* 64: 723–743.
- LACERDA, L. D., D. S. D. ARAÚJO, AND N. C. MACIEL. 1993. Dry coastal ecosystems of the tropical Brazilian coast. In E. van der Maarel [ed.], *Dry coastal ecosystems: Africa, America, Asia and Oceania*, 477–493. Elsevier, Amsterdam, Netherlands.
- LIEBIG, M., F. R. SCARANO, E. A. MATTOS, H. L. T. ZALUAR, AND U. LÜTTGE. 2001. Ecophysiological and floristic implications of sex expression in the dioecious neotropical CAM tree *Clusia hilariana* Schldt. *Trees Structure and Function* 15: 278–288.
- LÜTTGE, U. 1999. One morphotype, three phenotypes: sympatric species of *Clusia* with obligate C₃ photosynthesis, obligate CAM and C₃-CAM intermediate behaviour. *Plant Biology* 1: 138–148.
- MATHWORKS. 1997. MATLAB: the language for technical computing. Prentice Hall, Upper Saddle River, New Jersey, USA.
- MENDOZA, A., AND M. FRANCO. 1998. Sexual reproduction and clonal growth in *Reinhardtia gracilis* (Palmae), an understory tropical palm. *American Journal of Botany* 85: 521–527.
- MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- PICÓ, F. X., AND M. RIBA. 2002. Regional-scale demography of *Ramonda myconi*: remnant population dynamics in a preglacial relict species. *Plant Ecology* 161: 1–13.
- PIMENTEL, M. 2002. Variação espacial na estrutura de comunidades vegetais da formação aberta de *Clusia* no Parque Nacional da Restinga de Jurubatiba. R.J. D.Sc. thesis, Universidade Federal do Rio de Janeiro, Brazil.
- PINHEIRO, F., AND F. BORGHETTI. 2003. Light and temperature requirements for germination of seeds of *Aechmea nudicaulis* (L.) Griesebach and *Streptocalyx floribundus* (Martius ex Schultes F.) Mez (Bromeliaceae). *Acta Botanica Brasílica* 17: 27–35.
- QUINTANA-ASCENCIO, P. F., AND E. S. MENGES. 2000. Competitive abilities of three narrowly endemic plant species in experimental neighborhoods along a fire gradient. *American Journal of Botany* 87: 690–699.
- REINERT, F., A. ROBERTS, J. M. WILSON, L. RIBAS, G. CARDINOT, AND H. GRIFFITHS. 1997. Gradation in nutrient composition and photosynthetic pathways across the restinga vegetation of Brazil. *Botanica Acta* 110: 135–142.
- RIBA, M., F. X. PICÓ, AND M. MAYOL. 2002. Effects of regional climate and small-scale habitat quality on performance in the relict species *Ramonda myconi*. *Journal of Vegetation Science* 13: 259–268.
- SAMPAIO, M. C., L. E. PERISSÉ, G. AGUIAR DE OLIVEIRA, AND R. IGLESIAS RIOS. 2002. The contrasting clonal architecture of two bromeliads from sandy coastal plains in Brazil. *Flora* 197: 443–451.
- SCARANO, F. R. 2002. Structure, function and floristic relationship of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. *Annals of Botany* 90: 517–524.
- SCARANO, F. R., H. M. DUARTE, K. T. RIBEIRO, P. J. F. P. RODRIGUES, E. M. B. BARCELLOS, A. C. FRANCO, J. BRULFERT, E. DELÉENS, AND U. LÜTTGE. 2001. Four sites with contrasting environmental stress in southeastern Brazil: relations of species, life form diversity, and geographical

- distribution to ecophysiological parameters. *Botanical Journal of the Linnean Society* 136: 345–364.
- SMITH, L. B., AND R. J. DOWNS. 1979. Bromelioideae (Bromeliaceae). *Flora Neotropica Monograph* 14: 1493–2142.
- TULJAPURKAR, S. D., AND S. H. ORZACK. 1980. Population dynamics in variable environments. I. Long-run growth rates and extinction. *Theoretical Population Biology* 18: 314–342.
- WIJESINGHE, D. K., AND D. F. WHIGHAM. 1997. Costs of producing clonal offspring and the effects of plant size on population dynamics of the woodland herb *Uvularia perfoliata* (Liliaceae). *Journal of Ecology* 85: 907–919.
- WIKBERG, S., AND B. M. SVENSSON. 2003. Ramet demography in a ring-forming clonal sedge. *Journal of Ecology* 91: 847–854.
- ZALUAR, H. L. T., AND F. R. SCARANO. 2000. Facilitação em restingas de moitas: um século de buscas por espécies focais. In F. A. Esteves and L. D. Lacerda [eds.], *Ecologia de Restingas e Lagoas Costeiras*, 3–23. NUPEM, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.