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The contrasting clonal architecture of two bromeliads from sandy coastal plains in Brazil

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Summary

The vegetation of the Brazilian sandy coastal plains ('restingas') consists of vegetation patches of different sizes, separated by bare sand. Clonal growth seems to play an important role in this system, since this patchy resource-poor environment imposes several constraints on the flora. *Aechmea nudicaulis* and *Vriesea neoglutinosa* are two bromeliad species that occur in the restinga of Maricá, southeastern Brazil. The clonal growth patterns of these species were studied in order to understand their clonal architecture and ramet growth dynamics. For *A. nudicaulis*, we mapped six clonal fragments and measured the number of ramets produced by each mother-plant, rhizome length and branching angle. Height and diameter were measured in live plants. For *V. neoglutinosa*, we measured the number of ramets produced by each mother-plant and the respective branching angles. Leaf number, height, and diameter were recorded over a period of five months. For both species, variation in these parameters was correlated with life stage of the ramets. Clonal fragments of *A. nudicaulis* concentrate live ramets at the edge of vegetation islands, increasing ramet density. This strategy allows a single clonal fragment to potentially occupy a large area, forming large ramet systems. In contrast, the clonal growth of *V. neoglutinosa*, with ramets that develop only after sexual reproduction and arise inside the mother-plants, practically without spacer structures, lead to the formation of compact small clonal fragments, retaining their original site of occupation, maintaining the patch size.

Key words: clonal growth, clonal architecture, sandy coastal plains, restingas, *Aechmea nudicaulis*, *Vriesea neoglutinosa*.

Introduction

Clonal growth of plants results in the production of genetically identical descendants with the potential to become independent of each other. Clones with tightly aggregated ramets can be defined as 'phalanx' and those with dispersed distribution ramets as 'guerilla' strategists (Lovett Doust 1981). However, most species have a growth form between these two extremes (e.g., Lovett Doust 1981; Sackville-Hamilton et al. 1987).

Guerilla forms have ramets generally intermingled with other species whereas phalanx modules tend to form distinct clumps surrounded by co-specific modules (Schmid 1990). Phalanx forms tend to promote local persistence of the clone while guerilla forms tend to have a foraging function, establishing ramets predominantly in high quality sites (de Kroon & Schieving 1990; Herben & Hara 1997).

Clonal growth architecture of several taxa and growth pattern models have been studied and developed in recent decades (e.g., Bell & Tomlinson 1980; Cain 1990; Klimes et al. 1997). However, many plant families have not been investigated yet, such as the Neotropical family Bromeliaceae in which almost all species have some type of lateral expansion (Benzing 2000). Most of the information on clonal growth in bromeliads comes from growers who use clonal growth to propagate their collections (Menescal 1996). There are few studies regarding the clonal growth of bromeliads in the field (Freitas et al. 1998; Garcia-Franco & Rico-Gray 1995; Scarano et al. 1997).

Aechmea nudicaulis and *Vriesea neoglutinosa* are two clonal bromeliads that occur in the Brazilian sandy coastal plains, locally called 'restingas' (Fontoura et al. 1991). This habitat often shows a vegetation mosaic organized in patches of different sizes (Lacerda et al. 1993), separated (from each other) by bare sand, which imposes distinct physical constraints on the plants such as salinity, drought and heat (Franco 1998). Clonal growth seems to play an important role in this system. Few species are capable of germinating and establishing on bare sand (Liebig et al. 2001; Zaluar & Scarano 2000). Bromeliads potentially have an important impact in recruiting, establishing and growing of new species in the patches, as they represent a source of water (accumulated in their tank), nutrients (Hay & Lacerda 1980) and physical protection for the seedlings (Fialho & Furtado 1993). There is also another variant in the case of the bromeliads: the feeding of those plants takes place mostly through the leaves (Benzing, 1980). Also, some characteristics of the environment and of bromeliads should be considered: the patch interior is very different from the patch edge, mainly regarding nutrients, light intensity, temperature and humidity; the interior has more nutrients, better conditions of humidity and temperature but less light (Hay & Lacerda 1980).

Populations of *A. nudicaulis* and *V. neoglutinosa* are both found mostly at the edge of vegetation patches in the Maricá restinga, southeastern Brazil, but in quite different situations. Despite being closely related species, their clonal growth patterns have several differences. *V. neoglutinosa* rosettes are tightly aggregated, forming a densely packed clump around the edge of the entire vegetation patch. In contrast, *A. nudicaulis* rosettes are scattered along the patch edge, intermingling with other species. These small-scale distribution differences may be influenced by the clonal architecture of the two species. In this study we describe the contrasting clonal architecture and ramet growth of *A. nudicaulis* and *V. neoglutinosa* in the Maricá restinga.

Material and methods

Study site and study species

The study area was located in the restinga of Barra de Maricá, which lies 35 km east of the city of Rio de Janeiro, in Rio de Janeiro state, southeastern Brazil (22°57′N, 42°53′E). It is a dry coastal ecosystem, formed during the Quaternary. The vegetation in this area occurs on two beach ridges, approximately 5 km long: primary beach ridge (near the sea) and secondary beach ridge (near the lagoon), and in the depression between the ridges (Lacerda et al. 1993). The flora is distributed in patches of sizes ranging from <0.5 to $>5{,}000$ m^2. The study site was located on the secondary beach ridge, where *Aechmea nudicaulis* and *Vriesea neoglutinosa* occur, usually at the edge of patches.

A. nudicaulis and *V. neoglutinosa* are two tank-bromeliads (which holds water in the middle of the rosette) that belongs respectively to Bromelioideae and Tillandsioideae subfami-

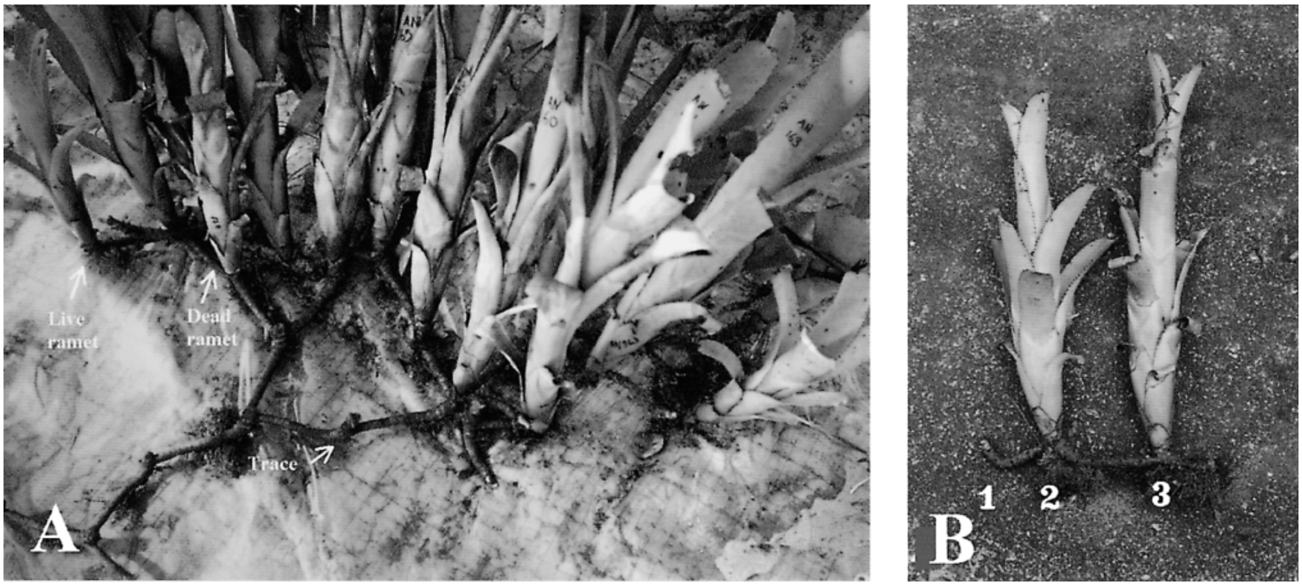

Fig. 1. A. Clonal fragments 5 (part) and 6 of *Aechmea nudicaulis* above the plastic grid, showing traces (without aerial part); dead ramet (with leaves totally dry); live ramet (with green leaves). B. Part of a clonal fragment of *A. nudicaulis*, showing a growth end with a very recently emitted ramet (location 1) still without roots. In location 2 there is a vegetative ramet and in location 3 a ramet with a dry infructescence beginning to die.

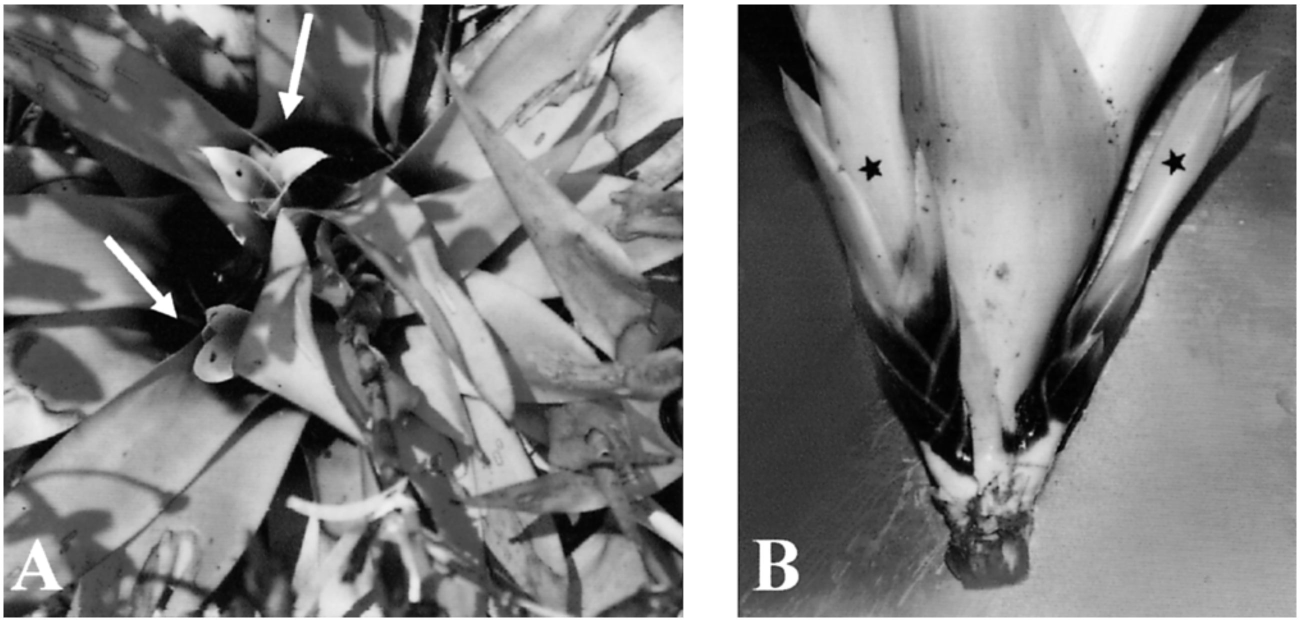

Fig. 2. A. Mother-plant of *Vrisea neoglutinosa* with two recently produced ramets inside it. The mother-plant leaves 'protect' the recently produced ramets (marked by arrows). B. Mother-plant of *V. neoglutinosa* without its lower leaves showing the insertion of the recently produced ramets (marked by asterisks) in the stem of the mother-plant, without any spacing structure.

lies. These two species, as most of other plants of Bromeliaceae family, flower only once during their life cycle and die after. How long does it take to die and when they produce ramets (before or after the flowering event) depends on the species.

Clonal growth of *Aechmea nudicaulis*

To study the clonal growth of *Aechmea nudicaulis* six clonal fragments were mapped. A clonal fragment was defined as a part of a clone with intact connections between two or more ramets. Rhizomes grew horizontally with little variation in depth below the surface, around 5 cm in depth.

The clonal fragments consist of live ramets, dead ramets (with dry leaves only) and ramet traces, that had lost their leaves but still maintain their roots (figures 1A and 1B). To map the clonal fragments, the sand was removed from around them, and a plastic grid was inserted below the rhizomes (figure 1A). The position of live and dead ramets and their traces were recorded on the grid. All mapped clonal fragments were located in the same patch. The following clonal growth parameters were measured: number of ramets produced by each mother-plant (a ramet that had already produced another), rhizome length, and branching angles.

To calculate the direction of growth in relation to the patch edge, branching angles between successive ramet locations were measured relative to north, where north was equal to 0°, east 90°, south 180° and west 270°.

In 25 clonal fragments that were not mapped, but had at least one flowering or fruiting ramet, we measured height and diameter ten centimeters from the base (basal diameter) of live ramets. Four life stages were assigned for the ramets: (1) vegetative, (2) flowering, (3) fruiting, (4) dry infructescence and (5) dead ramet.

Clonal growth of *Vriesea neoglutinosa*

Vrisea neoglutinosa ramet growth was monitored for six months to determine clonal growth. Since there were practically no spacer structures (figures 2A and 2B), it was impossible to measure rhizome length. Thus, only two clonal growth parameters were measured: number of ramets produced and approximate branching angle relative to north.

We also measured leaf number, height and diameter (at maximum leaf aperture) in the following life stages: (1) vegetative; (2) flowering; (3) fruiting ('mother-plant'); (4) recently produced ramet (see figure 5).

Results

Aechmea nudicaulis

The map of the six clonal fragments (figure 3) shows that there is considerable variation in *A. nudicaulis* clonal growth parameters measured (number of ramets produced by each mother-plant, rhizome length and branching angles). The live ramets of the clonal fragments were concentrated on the patch edge, as shown in figure 3. The rhizomes were produced sympodially from the base of older ramets.

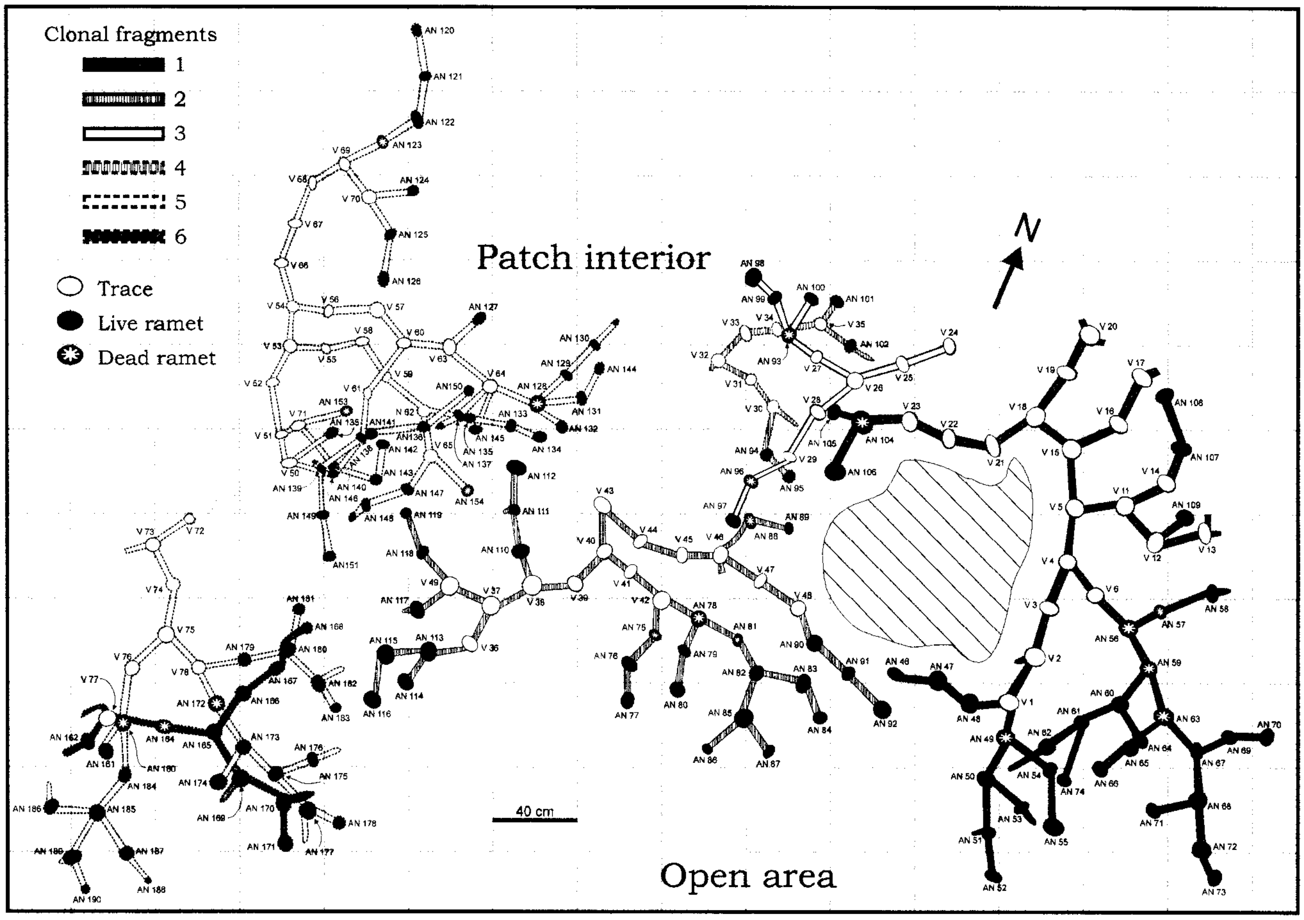

Fig. 3. Graphic representation of the six mapped clonal fragments of *Aechmea nudicaulis*, in the Maricá restinga. Each fragment is marked by a unique line pattern. Only ramets with obvious links were considered to belong to the same clonal fragment. The hatched area shows a large group of another bromeliad species (*Neoregelia cruenta*). Abbreviations: AN – locations of live ramets (in black) or dead ramets (in black with asterisk), V– locations with traces of the existence of a ramet (in white).

The maximum number of ramets produced by a mother-plant was 3, the mean and the standard deviation were 1.09 ± 0.80 (n = 213). Rhizome length values varied between 4 and 18 cm but the majority (73.53%) was between 10 and 14 cm long (11.83 ± 1.88, n = 204).

Branching angles relative to north showed great variation, ranging from 0° to 357°. Most angles (54.7%) were between 135° and 270°, which is between southeast and west, the direction of the patch edge. Only few ramets grew towards 0°–135° (19.1%) and 270°–360° (26.2%), which is between northeast and west, the interior of the patch.

Figure 4 illustrates the life stages of *A. nudicaulis*: vegetative, flowering, which will usually be fruiting within two weeks, dry infructescence (which probably flowered in the previous season), and dead ramet (which will deteriorate and become a trace). The capacity of older rhizomes to emit new ramets was not observed in *A. nudicaulis*.

In life stage characterization, significant differences between the vegetative and other life stages were found. Mean height and basal diameter of vegetative ramets were significantly lower than in the other life stages (table 1).

Vriesea neoglutinosa

Figure 5 is a schematic representation of the clonal growth of *V. neoglutinosa*, showing five life stages of the ramets. The first stage represents the ramets that have not flowered yet and have no connection with other ramets; these are vegetative ramets. Flowering ramets, with a sprouting inflorescence beginning to grow, represent the second stage. The third stage includes the fruiting ramets, or 'mother-plants'. In this stage the production of new ramets takes place exclusively within the mother-plants (see figures 2A and 2B), and only after

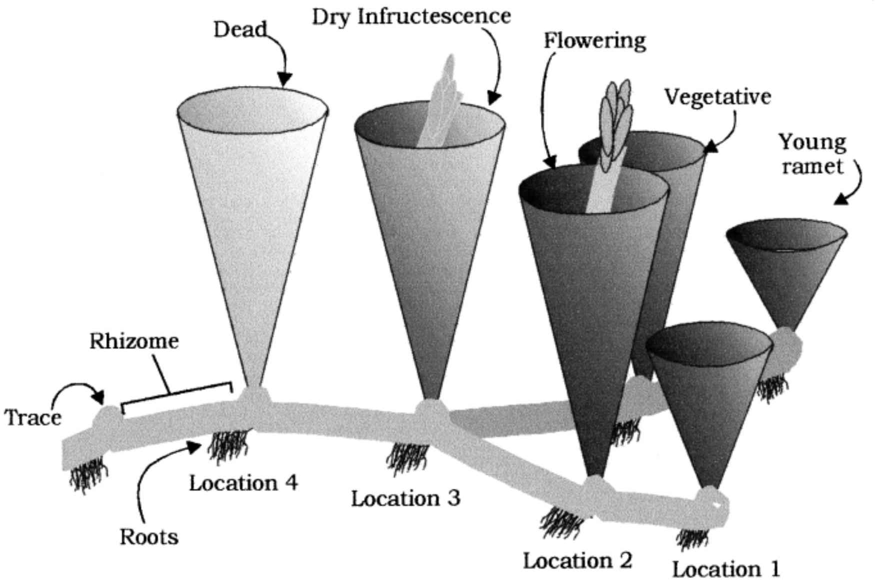

Fig. 4. Scheme of a clonal fragment with a flowering ramet of *A. nudicaulis*. This scheme illustrates location classification of the ramets and some of the life stages of *A. nudicaulis*: vegetative (in black), flowering (in black), dry infructescence (in gray) and dead ramet (in light gray).

sexual reproduction, after which the mother-plants begin to die. The fourth life stage includes young ramets still inside the mother-plants.

There were no measurements of the last stage mentioned in figure 5, since this stage is characterized by the total decomposition of the mother-plant. Here, the ramets were connected by dry rhizomes that were usually deteriorated, thus it was difficult to determine which ramets were originally produced by the same mother-plant.

Mean ramet production by a mother-plant was 2.17 ± 0.89 ramets (n = 143). The frequency distribution of ramet emissions varied considerably, but 50.79% of the mother-plants produced two ramets. Branching

Table 1. Mean and standard deviation of parameters used to characterize the life stages of clonal fragments with a flowering ramet of *Aechmea nudicaulis* in the Maricá restinga. For each parameter, values followed by the same letters are not significantly different from each other (Tukey HSD, $p < 0.05$); values of one-way ANOVA followed by *** $p < 0.001$.

Parameter	Vegetative	Flowering	Fruiting	Dry infructescence	F
n	24	23	4	9	
Height (cm)	25.40 ± 9.09 a	43.61 ± 7.11 b	43.80 ± 8.22 b	44.33 ± 5.34 b	26.47***
Basal diameter (cm)	3.18 ± 1.13 a	4.91 ± 0.66 b	4.50 ± 0.71 b	4.94 ± 0.77 b	17.01***

Table 2. Mean and standard deviation of the parameters used to characterize the life stages of *Vriesea neoglutinosa* in the Maricá restinga. For each parameter, values followed by the same letters are not significantly different from each other (Tukey HSD, $p < 0.05$); values of one-way ANOVA followed by *** $p < 0.001$.

Parameter	Vegetative	Flowering	Mother-plants	Recently produced ramet	F
Leaf number	20.78 ± 10.52 n = 238 a	26.73 ± 6.94 n = 77 b	15.02 ± 9.76 n = 126 c	11.68 ± 3.80 n = 600 d	172.51***
Height (cm)	46.33 ± 13.99 n = 238 a	51.95 ± 11.80 n = 77 b	33.76 ± 16.53 n = 122 c	29.70 ± 7.66 n = 601 d	162.04***
Diameter (cm)	41.20 ± 24.74 n = 238 a	50.48 ± 11.32 n = 77 b	31.09 ± 16.53 n = 116 c	29.56 ± 9.61 n = 449 c	49.31***

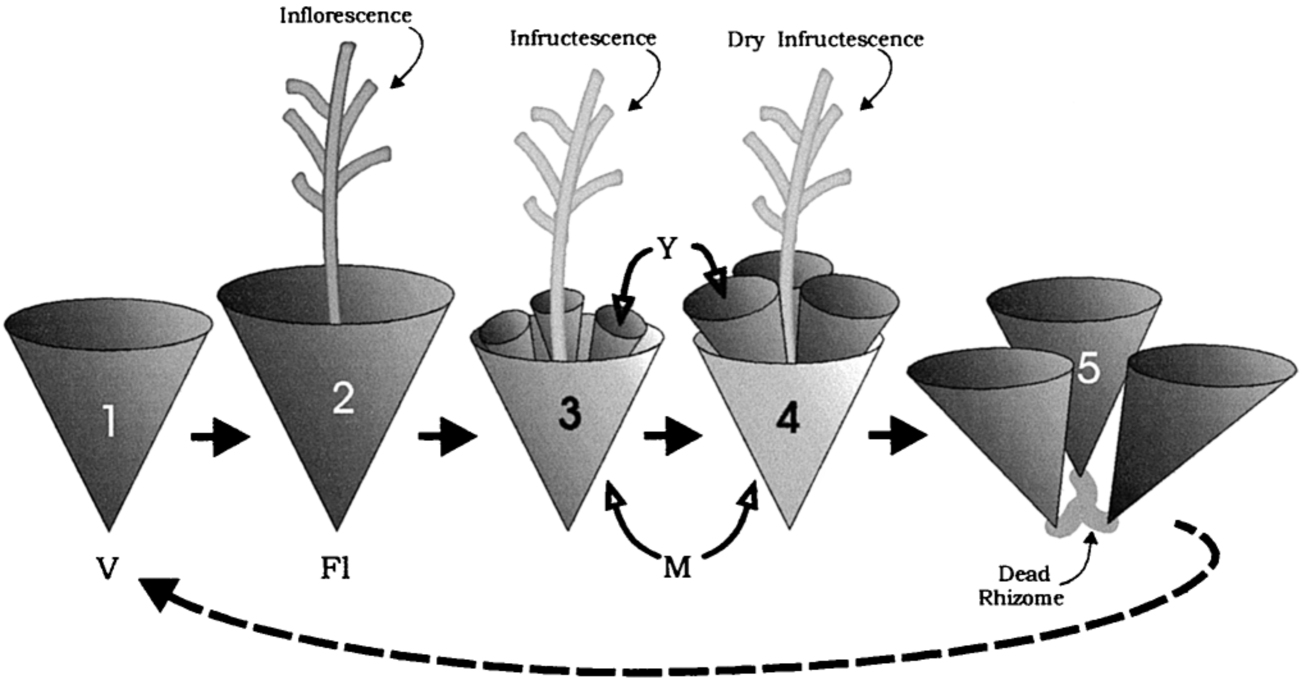

Fig. 5. Scheme of the clonal growth of *V. neoglutinosa*. Abbreviations: V – vegetative ramets (1); in this stage they have not yet flowered and have no connection with other ramets; Fl – flowering ramets, with inflorescence beginning to grow (2); M – Mother-plants (3), in this stage the emission of new ramets occurs after which the mother-plants begin to die; Y – Young ramets, still inside of the dead mother-plants (4); the last stage (5) is characterized by the total decomposition of the mother-plant. The ramets stay connected by a dry rhizome that deteriorates with time.

angles showed no marked direction of growth, at least relative to north, with mother-plants producing ramets in all directions.

For the morphological parameters measured (leaf number, height and diameter of the ramets), ramets in the flowering stage showed the highest values (table 2), indicating that the number of green leaves was greatest at this stage, and the ramets were taller and had greater diameters compared to the ramets in other stages.

Measurements were taken on the same mother-plants twice, and significant differences were found for all parameters (table 3). One month after the second measurement almost all mother-plants were dead, with the young ramets inside them continuing to grow, indicating that the young ramets will extend the initial site of occupancy of the mother-plant.

Differences in all parameters were also found for young ramets in all four measurements (table 3), the young ramets grew from one measurement to the other as expected.

Table 3. Mean and standard deviation of the sampling data of the life stages: (3) mother-plants and (4) young ramets of *Vriesea neoglutinosa* in the Maricá restinga. For each parameter, values followed by the same letters are not significantly different from each other (Tukey HSD, $p < 0.05$); values of one-way ANOVA followed by *** $p < 0.001$.

Life stage	Sampling date	n	Leaf number	Height	Diameter
Mother-plant	13-12-98	53	22.38 ± 5.91 a	39.57 ± 8.05 a	38.24 ± 9.66 a
	06-03-99	53	7.65 ± 6.96 b	27.55 ± 50.61 b	22.58 ± 18.90 b
	F		163.96***	18.40***	32.99***
Young ramet	10-01-99	152	7.93 ± 2.18 c	23.79 ± 6.86 c	–
	06-03-99	154	10.99 ± 2.77 d	28.15 ± 6.40 d	25.18 ± 8.75 d
	10-04-99	146	13.02 ± 2.80 e	32.44 ± 6.14 e	29.86 ± 8.73 e
	15-05-99	149	14.91 ± 3.28 f	34.64 ± 6.35 f	33.69 ± 9.44 f
	F		173.55***	83.63***	33.33***

Discussion

Clonal architecture in *Aechmea nudicaulis* and *Vriesea neoglutinosa* is very contrasting. *A. nudicaulis* can be placed near the guerilla extreme and *V. neoglutinosa* can be placed near the phalanx extreme. These differences generate distinct patterns of space acquisition for these bromeliads in the Maricá restinga. *V. neoglutinosa* forms small packed clonal fragments, probably with the capacity of exploration, almost without leaving the original patch, while *A. nudicaulis* forms large ramet systems, probably capable of greater spatial exploration.

A. nudicaulis produces large ramet systems with several interconnected ramets. Thus, a single clonal fragment can occupy a large area, and seems to have a direction of ramet growth (from the patch center to the edge). Clonal fragments were intermingled with other species. This result would explain why *A. nudicaulis* is usually found at the patch edge in the Maricá restinga, although it has to be taken into account that the measurements were done in a single patch.

V. neoglutinosa produces clonal fragments that remain connected for a short period of time, but due to the absence of spacer structures, they remain very close to one another. This strategy leads to the formation of clumped clonal fragments that retain their original site of occupation, like many clumped tillering grasses (JÓNSDÓTTIR & WATSON 1997).

The clonal fragments of *A. nudicaulis* develop large rhizome connected systems (see figure 3). For the maintenance of this system there must be physiological integration, not only to produce new ramets but also to maintain the net of underground rhizomes with nodes that have no aerial part, but do maintain their roots. The persistence of these older roots and rhizomes must contribute to the growth and survival of the clone and also to meet the demands of growing sink tips (DE KROON & SCHIEVING 1990; JÓNSDÓTTIR & CALLAGHAN 1990; MARSHALL 1990). Such structures (old rhizomes with nodes that maintain their roots) occur also in mayapple, *Podophyllum peltatum* (DE KROON et al. 1991; JÓNSDÓTTIR & WATSON 1997). In this species carbon is widely translocated from the point of fixation both acropetally into young growing ramets and basipetally into rhizomes and roots of the below-ground ramets. Intraclonal physiological integration has been demonstrated also for the above-ground stolon system of *Ajuga reptans* (DONG et al. 2002).

Observations and field experiments are needed to verify if *A. nudicaulis* follows the pattern found in mayapple and if there is clonal integration, between older roots and new ramets. Moreover, clonal integration seems to confer advantages in resource poor and salt stress environments (JÓNSDÓTTIR & WATSON 1997; PENNINGS & CALLAWAY 2000).

The clonal growth of *A. nudicaulis* shows some similarity to the clonal growth pattern described by GARCIA-FRANCO & RICO-GRAY (1995) for *Bromelia pinguin* in Mexico. In this species, which is from the same subfamily as *A. nudicaulis* (Bromelioideae), the production of ramets occurs independently of sexual reproduction, usually before flowering. The ramets are spaced by stolons, grow plagiotropically, and as many as three ramets are found interconnected. In the case of *A. nudicaulis* the ramets are spaced by rhizomes that also grow plagiotropically, but more ramets remain interconnected (<15), moreover, ramets in the vegetative phase are smaller and younger than the flowering, fruiting and dry infructescence ramets. Upon flowering, the ramet has reached its maximum height and diameters, which are maintained till death.

The architecture of *A. nudicaulis* shows considerable variation in the number of ramets produced by each mother-plant and in branching angles, but less variation in rhizome length.

V. neoglutinosa has well-defined life stages (figure 5 and table 2), with the emission of ramets only after sexual reproduction. The fast initial growth of the ramets and the death of the mother-plant a few months after the emission of the ramets indicates that resource flow probably occurs from the mother-plant toward the ramets (acropetally). Such unidirectional translocation, with the swift death of the mother-plant also occurs in *Glechoma hederacea* (SLADE & HUTCHINGS 1987).

In *V. neoglutinosa* the absence of spacer structures and roots in the recently produced ramets, and the location of the emission (inside the mother-plants), produces small, short-lived connections. This pattern produces clonal fragments that are physiologically integrated for a short period of time, and seem to have little capacity to explore favorable patches or to escape from unfavorable patches of the habitat, but also block the entrance and/or development of other species in the patches that it occupies.

The production of two new ramets was the most frequent case in *V. neoglutinosa*, occurring in 50% of the mother-plants. This shows the tendency of *V. neoglutinosa* to occupy more space after each new ramet production. Furthermore, the absence of a definitive branching angle of *V. neoglutinosa* apparently indicates that there is no direction in ramet growth, the main strategy being the occupation of space, apparently without choosing the direction. In contrast, *A. nudicaulis* strategy is to grow toward the patch edge, since most part of the angles relative to north were between 135° and 270°, directions that correspond to the patch edge.

The production of one new ramet was the most frequent case in *A. nudicaulis*, occurring in 42% of the mother-plants. However, the coefficient of variation of *A. nudicaulis* was higher than the coefficient of *V. neo-*

glutinosa, indicating that *A. nudicaulis* is more responsive to the environment than *V. neoglutinosa*. In the flowering stage sister ramets of *V. neoglutinosa* are still very close to one another, because of the lack of spacing between young ramets. On the other hand, *A. nudicaulis* has directionality in growth, having a tendency to increase ramet density in some preferred areas, allowing a single clonal fragment to occupy a large area. Although, it has to be taken into account that these results are based on data from a single vegetation period and significant differences can be expected in the performance of clonal plants in different years, in response to climate, patch dynamics and other factors (e.g. MEYER & SCHMID 1999; SALEMAA & SIEVÄNEN 2002). Hence, variation in the production of new ramets in *A. nudicaulis* and *V. neoglutinosa* is expected.

Thus, the influence of these two species on patch dynamics probably is very distinctive. *V. neoglutinosa* apparently retards patch expansion, while *A. nudicaulis* seems to have a positive impact on expansion at the patch edges. Patches with different compositions would then be directed to expansion or maintenance of patch size. However, further studies on population structure and dynamics of these two species are needed to quantify their influence on patch dynamics. Moreover, other studies are needed also to elucidate the 'age-structure', e.g. (i) How long does a ramet remain in each life stage? (ii) When does it flower? (3) How long do the connecting spacers between two ramets last? (4) What is the maximum age of a fragment from establishment to death? Such data would allow a better analysis of the structure, dynamics and architecture of these two clonal plants and possibly also provide insights in the structure of the habitat. To answer these questions long-term studies are needed.

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