# Effect of rosette size, clonality and spatial distribution on the reproduction of *Vriesea carinata* (Bromeliaceae) in the Atlantic Forest of Paraná, southern Brazil

**Marcelo Aparecido de Souza Silva**[1,2] **and Isabela Galarda Varassin**[3,*]

## ABSTRACT

Plant size and clonality are important traits for explaining the reproductive effort of clonal plants. Larger plants can invest more resources into reproduction, and clonality is known to increase reproductive effort. Moreover, reproductive effort is influenced by environmental variation, and so the spatial distribution of plants may affect plant reproductive effort. We investigated the effect of plant size, clonality and spatial distribution on the reproductive effort of *Vriesea carinata* in the Atlantic Forest in the state of Paraná, Brazil. We marked twenty individual plants and measured their rosette size, biomass and number, as well as rosette reproductive effort (number of flowers, fruits and seeds). We also evaluated the relationship between reproductive effort and spatial distribution of plants. Reproductive effort did not correlate with size, whereas greater clonal growth contributed to a lower reproductive effort because rosettes within clones that had more rosettes set fewer flowers. We found that plants growing closer to each other exhibited similar reproductive efforts independently of vegetative traits, because reproductive traits were spatially autocorrelated. In *Vriesea carinata,* the main drivers of reproductive effort are clonality, which decreases flower production, and spatial factors, which result in greater similarity in reproductive efforts among more proximate plants.

**Keywords:** clonal growth, morphological variation, reproductive effort, RNSM, *Vriesea*

## Introduction

Plant size and biomass are correlated with the allocation of resources for reproduction (Aarssen & Taylor 1992), and thus are important for plant fitness (Bazzaz 1997). Resource allocation for reproduction is defined as the proportion of resources, such as energy or biomass, invested by a plant in vegetative structures versus those invested in reproductive structures, such as flowers, fruits, seeds, floral stems and bracts (Abrahamson & Caswell 1982; Bazzaz *et al.* 1987). Flowers, fruits, and seeds are obvious reproductive parts

of plants, but other structures, such as floral stems and bracts, may also be involved in resource allocation (Bazzaz 1997). The amount of resources invested in reproduction is closely correlated with plant size and biomass, such that bigger/heavier plants invest more in flowering than smaller plants (Aarssen & Taylor 1992). For bromeliads, the amount of resources invested in reproductive structures is also correlated with the size of the plant, but not always proportionally (Mantovani & Iglesias 2009).

A combination of sexual reproduction, via seed production (Martinelli 1997), and vegetative reproduction,

[1] Pós-graduação em Conservação da Natureza e Educação Ambiental, Pontifícia Universidade Católica do Paraná, 80215-901, Curitiba, PR, Brazil
[2] Associação Franciscana de Ensino Senhor Bom Jesus, Nestor Victor, 910, 82620400, Curitiba, PR, Brazil
[3] Departamento de Botânica, Universidade Federal do Paraná, 81531-980, Curitiba, PR, Brazil
[*] Corresponding author: isagalarda@gmail.com

via clonal propagation, is common among bromeliads (Benzing 2000). Clonal reproduction assures the persistence of local populations by skipping sterility or a lack of pollinators (Reitz 1983; Sampaio *et al.* 2002). In clonal plants, parental and daughter ramets are physiologically integrated (Pitelka & Ashmun 1985), which results in the transfer of resources that improves clonal growth and survival (Roiloa *et al.* 2010). Clonality, in turn, may also increase flower production (Demetrio *et al.* 2014).

In bromeliads, the spatial distribution of plants affects their sexual reproductive success (Scrok & Varassin 2011). The spatial distribution of bromeliads can be influenced by the local environment, including such factors as the presence of suitable substrate, light, temperature and humidity (Cogliatti-Carvalho *et al.* 2001). These environmental features are often spatially structured (Cottenie 2005) and may influence plant reproduction in a complex way. For example, neighboring individuals may compete for pollinators (Grindeland *et al.* 2005; Brys & Jacquemyn 2010), and so changes in fecundity may be related to variation in spatial arrangement (Aarssen & Taylor 1992; Scrok & Varassin 2011). Furthermore, the balance between clonal and sexual growth in clonal plants may change according to microenvironmental heterogeneity (Coelho *et al.* 2008a; Izquierdo & Piñero 1998). Considering that neighboring individuals are under the same microenvironmental conditions, the balance between clonal and sexual growth would be expected to be similar. Therefore, it is expected that neighboring individuals would be similar in terms of morphology, reproduction (Jacquemyn & Honnay 2008) and/or kinship (Kittelson & Maron 2000). If so, this would be reflected in a spatial autocorrelation between these traits.

Reproductive traits for both pollination and dispersal are considered important drivers of the diversification of Bromeliaceae (Givnish *et al.* 2014). These traits are associated with an epiphytic habitat and include: 1) sexual reproduction coupled with bird-pollination (mostly hummingbirds) and 2) presence of "entangling seeds" (i.e., those able to attach to a host), such as wind-dispersed comose seeds or animal-dispersed seeds from fleshy fruits. *Vriesea* is the third largest bromeliad genus with approximately 280 species (Costa *et al.* 2015), which have monocarpic and clonal reproduction *via* axillary buds in the basal leaf sheaths (Costa *et al.* 2014), and are mostly pollinated by hummingbirds (Araújo *et al.* 1994; Sazima *et al.* 1995a; 1996; Martinelli 1997; Machado & Semir 2006; Varassin & Sazima 2012), but also by bats (Sazima *et al.* 1995b; 1999; Martinelli 1997; Kaehler *et al.* 2005), bees (Kaehler *et al.* 2005) and butterflies (Scrok & Varassin 2011; Varassin & Sazima 2012). The comose seeds are dispersed by wind (Costa *et al.* 2015).

Our study model was *Vriesea carinata* Wawra, which occurs in the Atlantic Forest of Paraná in southern Brazil. We hypothesized that size and clonality are important traits for explaining the reproductive effort (number of flowers, fruits and seeds) of this bromeliad. We also hypothesized

that due the fact that environmental variation is often spatially structured, the spatial distribution of plants will explain reproductive effort in *V. carinata*. The following questions guided our study: 1) Does rosette size increase sexual reproductive effort in *V. carinata*? 2) Does clonal growth (number of rosettes) increase sexual reproductive effort in *V. carinata*? 3) Will plants distributed more closely have similar sexual reproductive effort?

## Materials and methods

### Study site

We carried out this study at Reserva Natural Salto Morato (hereafter RNSM), which belongs to Fundação Grupo Boticário de Proteção à Natureza (FGBPN). It is located in Guaraqueçaba in the state of Paraná of southern Brazil within a broader conservation unit, the Environmental Protection Area of Guaraqueçaba (25°10'44"S, 48°18'42"W). RNSM encompasses 2,340 ha of Atlantic Forest and varies in elevation from 15 to 918 m. According to the Koeppen system, the climate of the region is Af – tropical super humid without drought, with an average annual temperature of 21°C and average monthly temperatures ranging between 17 and 25°C. The summer (November to March) is warm and rainy, whereas the winter is dry and cold (FGBPN 2011).

Fieldwork was carried out from June to August 2012, when we selected and marked 20 individual plants of *Vriesea carinata* Wawra close to a trail in the reserve (ca. 25°18'15"S, 48°30'72"W).

### Plant species

*Vriesea carinata* Wawa is usually an epiphytic bromeliad. It occurs in humid and well-preserved sites (Martinelli *et al.* 2008), and has a broad distribution in the Atlantic Forest, occurring from the state of Rio Grande do Sul to the states of Minas Gerais and Espírito Santo (Forzza *et al.* 2016). It flowers from April to October, with a peak from June to August, has flowers of various shades of red (Smith & Downs 1977; Wanderley & Martins 2007; Martinelli *et al.* 2008) with each rosette producing a single inflorescence. Anthesis occurs from 07:30 to 17:00, and lasts a single day (Araújo *et al.* 1994; Machado & Semir 2006; Piacentini & Varassin 2007). At the study site, *Vriesea carinata* is pollinated by hummingbirds (Piacentini & Varassin 2007).

Individuals of *V. carinata* at the study site have one to five rosettes (pers. obs.). Clonal growth can be visually followed by the growth of axillary buds at basal leaf sheaths of the parent plant. The shoots are born outside the rosettes, and produce clumps of rosettes. Following the order of axillary shoots, rosette age hierarchy, from the oldest to the youngest daughter rosettes, was determined by the order of sexual maturity. Rosettes linked by stolons were considered ramets

of the parent plant (genet). Therefore the individual can be either an isolated rosette or groups of rosettes linked by stolons. In our study, we considered the plants as different individuals when they were: i) not linked by stolons, ii) at least two meters apart and iii) on different tree trunks. A voucher was deposited at the Museu Botânico Municipal de Curitiba (voucher number 390642).

## Sexual reproductive effort

For each plant we selected a single rosette, the oldest one, to estimate sexual reproductive effort. For that rosette we measured inflorescence length and counted the total number of flowers, total number of fruits, and the number of seeds per fruit. The number of fruits produced by the rosette was counted until the end of the flowering period in August. To estimate seed number we sampled three fruits from a single rosette from each individual plant: one fruit from the base of the infructescence, one from the middle and one from the apex. Since the seeds are very small and abundant, we estimated the number produced in each of the three fruits based on the mass of 20 seeds and extrapolated to the total mass of the fruit. The seeds were weighed on an analytical scale with 0.001g accuracy.

## Rosette size, clonality and spatial distribution

We measured rosette size in two ways: 1) diameter of each rosette from the most extreme leaf (apex) on one side to the most extreme leaf (apex) on the opposite side; and 2) length of the most basal leaf. The rosettes, composed of leaves and inflorescence, were dried for 96h at 60°C and subsequently weighted on an analytical balance.

Since *Vriesea carinata* may have one to five rosettes, we marked plants with different levels of clonal growth or clonality (estimated here as the number of rosettes); four plants had isolated rosettes (one rosette), four plants had two rosettes, four had three rosettes, four had four rosettes and four had five rosettes (totaling 20 plants). All plants were georeferenced using a high precision 62s model GPS; plants were at least two meters apart to avoid georeferencing error as indicated by the GPS manual.

## Data analysis

To test if larger size is related to an increase in sexual reproductive effort, we used a partial correlation analysis between vegetative traits (rosette diameter, basal leaf length and biomass) and reproductive traits (inflorescence length, number of flowers, fruits, and seeds).

To test if increased clonality (plants with more rosettes) is related to an increase in sexual reproductive effort, we analyzed the relationship between the level of clonal growth and reproductive traits (inflorescence length,

number of flowers/rosette, fruits/rosette and seeds/fruit) with a regression analysis. Since the number of fruits was correlated with the number of flowers produced by each rosette ($r2 = 0.68$; $F1,18 = 41.51$; $P < 0.0001$), we used the regression residuals between those two variables to test the effect of the number of rosettes on the number of fruits, controlled by the number of flowers.

To analyze whether reproductive effort is related to spatial distribution, that is to test for the presence of spatial autocorrelation in our data, we performed a Mantel test (Mantel 1967; Legendre & Fortin 1989). We first used a Mantel correlation between the matrix of vegetative variables and the spatial matrix to test whether vegetativeley similar plants grew closer to each other, possibly due to a kinship or dispersal effect. We tested for spatial autocorrelation in reproduction traits with a partial Mantel correlation using the Pearson coefficient. In the Mantel test, we compared the reproductive data matrix (number of flowers, fruits, and seeds) to the spatial data matrix (latitude and longitude transformed into geodesic distances), and used the vegetative data matrix (number of rosettes, diameter, basal leaf length, and dry biomass weight) as a control for rosette size. The matrix of vegetative variables was standardized and the matrix of reproductive variables was log-transformed. We converted all matrices to dissimilarity matrices, using the Euclidean distance for the matrix of latitude and longitude and the matrix of vegetative variables, and the Bray-Curtis distance for the matrix of reproductive variables. We made 10,000 permutations to estimate the significance of the partial Mantel correlations. All analyses were performed in R software Version 2.14.1 (R Development Core Team 2011).

# Results

The number of flowers, fruits and seeds was similar in rosettes of different sizes (diameter, basal leaf and biomass). Rosettes with higher biomass produced larger inflorescences (Tab. 1). Rosettes with more flowers produced more fruits (Tab. 1).

Higher clonality decreased flower production since rosettes within plants with more rosettes produced fewer flowers ($r2 = 0.51$; $F1,18 = 21.02$; $P = 0.0002$; Fig. 1A). The number of fruits produced by a rosette, controlled for the number of flowers, as well as the number of seeds produced by a fruit, was similar in plants with different numbers of rosettes ($r2=0.09$; $F1,18=2.84$; $P = 0.1091$; Fig. 1B; $r2 = -0.02$; $F1,18 = 0.47$; $P = 0.5034$, respectively).

Plants with similar number of rosettes, and similar diameter, basal leaf length, and dry biomass weight (i.e. vegetative traits) did not show spatial autocorrelation ($r_{Mantel} = 0.0153$; $P = 0.3997$). On the other hand, plants with similar reproductive traits - rosettes with a similar number of flowers, fruits, and seeds - were found growing closer to each other, because those reproductive traits of *V. carinata* were

**Table 1.** Partial correlations (*r*) between vegetative traits (rosette diameter, basal leaf length, dry biomass) and reproductive traits (number of flowers, fruits and logarithm of the number of seeds and inflorescence length). P-values in parentheses. Bold for P<0.05.

| | Number of flowers | Number of fruits | Logarithm of the number of seeds | Inflorescence length |
|---|---|---|---|---|
| **Number of fruits** | **0.7067 (0.0069)** | | | |
| **Number of seeds (log)** | 0.2771 (0.3594) | -0.4578 (0.1157) | | |
| **Inflorescence length** | -0.2154 (0.4797) | 0.0359 (0.9073) | -0.0313 (0.9191) | |
| **Diameter** | -0.2661 (0.3795) | 0.3228 (0.282) | -0.0737 (0.8109) | 0.3383 (0.2582) |
| **Basal leaf length** | 0.0243 (0.9372) | -0.0729 (0.8129) | -0.0307 (0.9207) | -0.5073 (0.0768) |
| **Dry biomass** | -0.0087 (0.9775) | 0.3146 (0.2951) | 0.1687 (0.5817) | **0.5908 (0.0335)** |
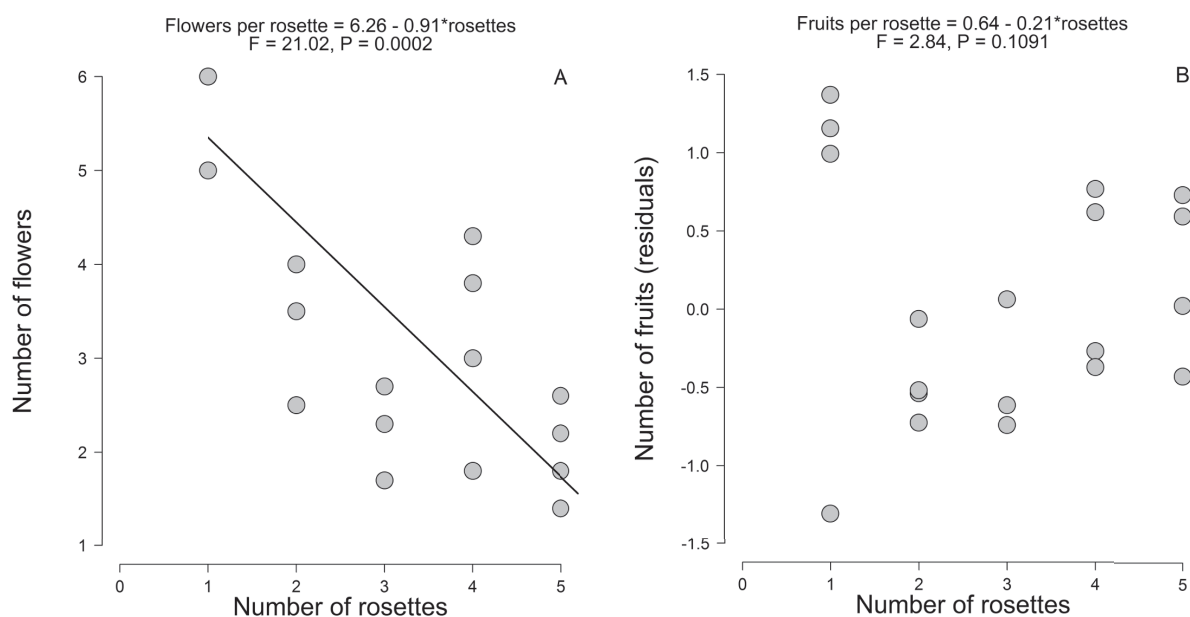


**Figure 1.** Relationship between reproductive traits: (A) number of flowers and (B) number of fruits (residuals) in the bromeliad *Vriesea carinata* as a function of the number of rosettes, RNSM.

spatially autocorrelated. The autocorrelation on reproductive traits was independent of plant size distribution ($r_{\text{Mantel partial}}$ = 0,1314; *P* = 0.0312).

## Discussion

The reproduction of *Vriesea carinata* was influenced by clonality. Plants with stronger clonal growth (larger number of rosettes) produced fewer flowers per rosette, but the fruit set per flower was the same among plants with different clonal growth. On the other hand, there was no relationship between reproductive effort and rosette size or biomass. In *V. carinata* there was a spatial correlation between reproductive traits regardless of vegetative traits.

In *V. carinata* the number of fruits was related to the number of flowers produced by the rosette, but not to size or biomass. Bigger plants do not result in higher reproductive effort even when biomass was measured with inflorescences. The reproductive effort in *V. carinata* differs from what has been reported for other species, because flower production is frequently correlated with plant size, which usually increases with increased resource availability (Ågren *et al.* 2008; Dauber *et al.* 2010). In bromeliads, sexual reproduction tends to increase with an increase in plant size (Benzing 1981; Hietz *et al.* 2002; Mondragón *et al.* 2004; Mantovani & Iglesias 2009). For *V. carinata*, factors such as the clonality discussed below might be causing an increase in competition for resources and limiting the amount invested in flower production, thereby uncoupling the effect of rosette size on reproductive effort.

The negative effect of clonality on reproductive effort

indicates a negative effect on sexual reproduction resulting from vegetative (clonal) reproduction. It is usually considered that there is a positive relationship between resource availability and the conversion of those resources into vegetative growth and finally into reproduction (Bazzaz *et al.* 1987). In this case, resource transfer to younger rosettes would enhance flower and fruit production. Nevertheless, physiological integration between ramets and clonal plants under a more uniform environment may have a negative effect on offspring biomass (Alpert 1999); this could explain why higher clonal growth results in decreased investment in flower production in *V. carinata*. Furthermore, when conditions are not favorable for sexual reproduction, clonal reproduction provides reproductive assurance (Vallejo-Marín & O'Brien 2007; Coelho *et al.* 2008b) and the maintenance of plant populations. In general, the persistence of clonal plants in the long term depends on a balance between the survival of genets through clonal growth after population establishment and recruitment through sexual reproduction (Jacquemyn *et al.* 2006).

The absence of spatial structure in the distribution of plants sharing the same vegetative traits indicates that plants more distantly located have more similar vegetative traits (related to size) than those growing closer. This may be due to the uniform environment where the plants are growing or to the physiological integration of clones buffering the negative effects of microhabitats (Roiloa *et al.* 2010), and resulting in similar-sized plants despite spatial/environmental variation. On the other hand, *V. carinata* has spatial structure associated with reproduction, since plants close to each other were similar in terms of number of flowers, fruits and seeds. This may be a result of spatial structuring of the environment in which the plants grow, in terms of humidity, substrate and light availability, since local abiotic conditions are usually involved with variation in reproductive efforts (Ågren *et al.* 2008). Even small variation in tree crowns due to light availability may change the number of flowers produced by a plant (Maia *et al.* 2013). Indeed, *Aechmea distichantha* bromeliads growing under sunny conditions had a larger reproductive effort than those in shaded conditions, when controlled for bromeliad size (Scrok & Varassin 2011). It is also possible that aggregated individuals are genetically more closely related (Lovett-Dust 1981; Izquierdo & Piñero 1998; Canela & Sazima 2003; Jacquemyn & Honnay 2008) and thus have the same reproductive potential. Plant spatial distribution can also change the patterns of pollen distribution, and closer conspecific plants have been found to have higher pollen load and higher seed set (Brys & Jacquemyn 2010). On the other hand, for clonal plants, intensive clonal growth should increase self-pollen deposition and consequently should reduce the chance of cross-fecundation, decreasing female fecundity (Clark-Tapia *et al.* 2005; 2006; Dorken & Drunen 2010). Both situations would result in similar fruit/seed production in plants growing closer to each other.

Hence, *V. carinata* rosettes within clones with more rosettes set fewer flowers. On the other hand, rosettes with more flowers set proportionally the same amount of fruits as rosettes with fewer flowers. Plants growing closer to each other have similar reproductive efforts and this spatial distribution was independent of vegetative traits. Indeed, bromeliad size had no effect on reproductive effort, and thus spatial structure of vegetative and reproductive traits we not correlated. In *Vriesea carinata,* the main drivers of reproductive effort are clonality, which decreases flower production per rosette, and spatial factors, which result in greater similarity of reproductive efforts among closer plants.

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