

Plant density influence on life history traits of a perennial herb in rocky outcrops, southeastern Brazil

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ABSTRACT - Rocky outcrops support a great diversity of edaphic conditions and associated vegetation mosaics greatly determined by factors like local topography and micro-environment. The vegetation is grouped, and clonal plants may form patches with different densities. Density-dependent responses are an important component of organism's life-histories. We evaluated the density effects on *Vellozia albiflora* traits. We settled 20 monospecific patches of *V. albiflora* with different densities and sampled vegetative and reproductive traits. We compared traits between plants experimenting densely crowded and uncrowded conditions. *V. albiflora* rosettes present larger sizes and higher production of sexual reproductive structures in high densities. We concluded that *V. albiflora* probably allocates more resources to sexual reproduction in response to high-density conditions, which may allow a higher survival of offspring, since seeds are able to endure in soil and germinate under better density conditions, whereas the propagules generated by asexual reproduction must establish right after their production.

Keywords: clonal plant, inselbergs, persistence strategies, *Vellozia albiflora*

RESUMO - Influência da densidade de plantas em traços de história de vida de uma herbácea perene em afloramentos rochosos, no sudeste brasileiro. Afloramentos rochosos apresentam grande variedade de condições edáficas e mosaicos vegetacionais, determinados por fatores como topografia local e microambientes. A vegetação ocorre agrupada, e plantas clonais formam manchas com diferentes densidades. Respostas dependentes de densidade são importantes nas histórias de vida dos organismos. Avaliamos efeitos da densidade em traços de *Vellozia albiflora* Pohl. Marcamos 20 manchas de *V. albiflora* com diferentes densidades e amostramos altura, diâmetro, número de folhas, flores e escapos e comprimento dos escapos para todas as rosetas em cada mancha. Comparamos os traços amostrados entre as condições de densidade. Rosetas de *V. albiflora* foram maiores, com maior quantidade de estruturas reprodutivas sexuadas em altas densidades. *V. albiflora* provavelmente aloca mais recursos para a reprodução sexuada em resposta à alta densidade, que pode proporcionar maiores chances de sobrevivência da prole, porque sementes podem aguardar por melhores condições de germinação, como densidades menores, ao contrário da prole da reprodução assexuada.

Palavras-chave: estratégias de persistência, inselbergs, planta clonal, *Vellozia albiflora*

INTRODUCTION

The vegetation of rocky outcrops is grouped in islands formed by one or more species fixed directly on the rocks or in shallow soils (Conceição & Giulietti 2002, Porembski 2007). These vegetation mosaics are determined by factors like local topography and micro-environmental characteristics (Benites *et al.* 2007). Rocky outcrops support very specialized vegetation and are associated to stressing habitats (Scarano *et al.* 2001) where monocotyledonous mats are often found as patches surrounded by bare rock (Medina *et al.* 2006, Porembski 2007). Plant species in these mats are frequently found at different densities. Some plant groups show clear specialization for survival in these environments, such as in the case of the resurrection plants

in South America, mainly Cyperaceae and Velloziaceae (Meireles *et al.* 1997).

Many studies deal with density effects on plants life history traits, and they show very different plastic responses depending on the life history trait analyzed. Regarding morphology, leaves size, for example, were greater in high-density conditions than in low-density conditions for *Pistia stratiotes* L., *Eichhornia crassipes* (Mart.) Sölm., *Sagittaria montevidensis* Cham. & Schldtl. (Coelho *et al.* 2005, Alvarenga *et al.* 2013, Demetrio *et al.* 2014a). In relation to plants reproductive modes, clonal plants would allocate more energy to sexual reproduction, which should increase at the expense of clonal growth, with increases in density. At low densities, increased allocation to clonal growth would facilitate rapid spread with low risk. On the

other hand, at higher densities local conditions for growth would be unfavorable because of crowding (Abrahamson 1975). These results were corroborated by Coelho *et al.* (2005) and Komac & Alados (2012). High density can also generate different effects on plant population size, since there will be a bias in the reproductive mode used by the individuals submitted to different density conditions (Plaza *et al.* 2012).

Various studies focusing on plant ecology in Brazilian tropical rocky outcrops have been done (Porembski *et al.* 1998, Ribeiro & Fernandes 2000, Scarano *et al.* 2001, Medina *et al.* 2006, Coelho *et al.* 2014, Demétrio *et al.* 2014b), and despite one of them showed the relationship between *Vellozia* height and flowers number to herbivores abundance (Landau *et al.* 1998), none of them addressed plants life history traits and relations with density. Our study aimed to evaluate the density-dependent responses of life history traits of a perennial herb, *Vellozia albiflora* Pohl (Velloziaceae), by testing the following hypotheses: (i) The number of reproductive structures (flowers and flower scapes) will be higher in high plant densities, and (ii) The flower scapes length will be lower in high plant densities and, (iii) The height and diameter of the plants will be lower in high plant densities.

MATERIALS AND METHODS

Study area

We carried out the study at gneiss outcrops of Morro do Cruzeiro (43°22'10"W; 19°53'23"S), in São Gonçalo do Rio Abaixo, a city located in Minas Gerais, Brazil (Fig. 1). The study area is part of the Estação de Pesquisa e Desenvolvimento Ambiental de Peti (EPDA-Peti), a particular area belonging to the Energetic Company of Minas Gerais (CEMIG). The area presents a rugged relief

formed by counterforts of the Espinhaço Mountain Range. The local vegetation is mainly composed by riparian forests, seasonal semideciduous forests and herbaceous vegetation covering gneiss rocky outcrops (Pedralli & Teixeira 1997, Borba & Braga 2003).

Terminology

Clonal plants may present offspring production by sexual and asexual ways. Harper (1977) defined the produced individuals as genets and ramets, respectively. However, these two distinct categories of individuals can be related to different structures depending on the studied taxa. A genet is an individual formed through sexual reproduction by seed formation. The ramet, on the other hand, is defined as an individual formed by vegetative growth and is physiologically independent of its parental plant.

In the case of our study, we only sampled populations with ramets forming clones. In *Vellozia albiflora* these ramets are morphologically characterized by their habit of growing in a rosette from which scapes with flowers appear. In this species, the seedling originating from seed besides being a genet is also a ramet. A group of ramets produced vegetatively and connected by rhizomes also form a genet. Therefore, in this species, a genet can contain one (individual ramet) or several ramets (colonies of connected ramets) linked by rhizomes. We considered the rosette (shoot forming) and its associated root system as a ramet. Hereafter we call all the ramets as rosettes.

Study species

Velloziaceae is a botanical family, which occurs mainly in rupestrian grasslands and rocky outcrops. The plants belonging to this family are perennial organisms that usually



Fig. 1. Map of the studied area, showing the location of Estação de Pesquisa e Desenvolvimento Ambiental de Peti on Minas Gerais State, Brazil.

inhabit shallow and poor soils with higher organic matter content and a low proportion of small particles (Rapini *et al.* 2008). The family is very representative in the rocky outcrops vegetation of the Espinhaço Range, southeastern Brazil (Giulietti & Pirani 1988), a region with very high level of endemism, probably associated with the altitudinal isolation (Alves & Kolbek 1994).

Vellozia albiflora (Fig. 2a), popularly known as “canelade-ema”, is an herbaceous plant well distributed along the Espinhaço Range, the Órgãos Range and the Mantiqueira Range (Mello-Silva 2009). It usually occurs in rocky outcrops and rupestrian grasslands. In our study, clonal specimens of *V. albiflora* were found forming vegetation islands in gneiss rocky outcrops.

Plant sampling

We performed one sampling event in October 2010, when 20 monospecific vegetation mats (patches) formed by *V. albiflora* rosettes were sampled. Some specimens were in full blooming, while others showed only flower scapes. We selected 10 mats with low density of rosettes and another 10 with high density of rosettes, and sampled the rosettes by using a sampling quadrat of 2 m². Density of *V. albiflora* was recorded by estimating the percentage of the quadrat covered by vegetation: < 30% of the quadrat characterizes low-density conditions, and > 60% of the quadrat covered by vegetation characterizes high-density (Coelho *et al.* 2005; Alvarenga *et al.* 2013) (Fig. 2b). Inside each quadrat we took the following measures for all rosettes of *V. Albiflora*: 1) vegetative height; 2) diameter; 3) number of leaves; 4) number of reproductive structures (flowers and scapes – in this sense, some plants presented scapes, but not

flowers, indicating that the sexual reproduction occurred in a recent past); 5) maximum length of the flower scape.

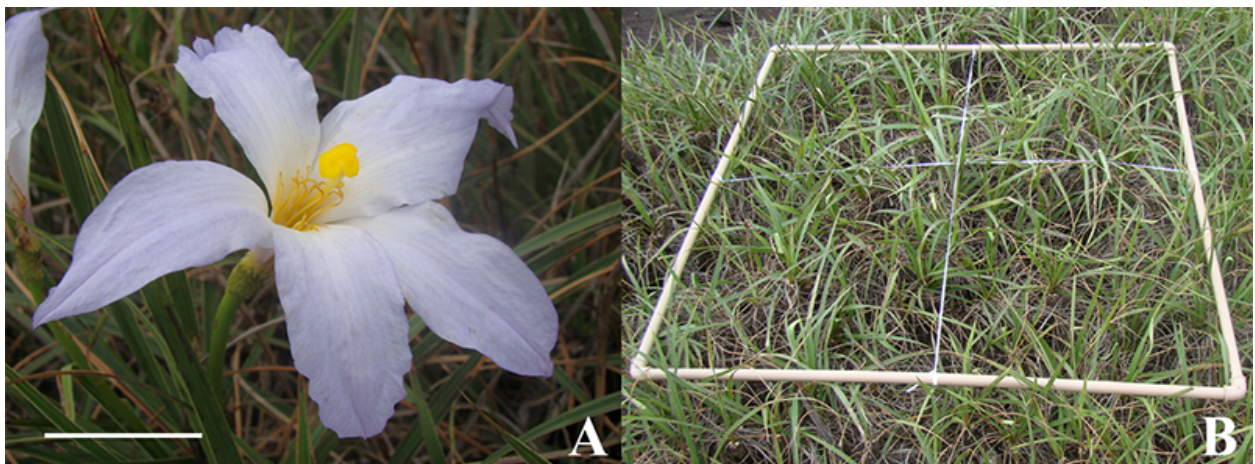
Data analysis

All variables of morphological traits were tested for normality with Shapiro-Wilk tests. To evaluate the influence of plant density on *V. albiflora* life history traits, we applied GLMM's with Gaussian distribution for all life history traits that were measured. In order to account for local differences among plant mats, for every model, the mat was inserted as a random factor. The level of plant density on the mat (high or low) was inserted as a fixed variable, and the measured life history traits were used as response variables. All analyses were carried on R Environment (R Core Team 2017), using the package lme4 (Bates *et al.* 2015).

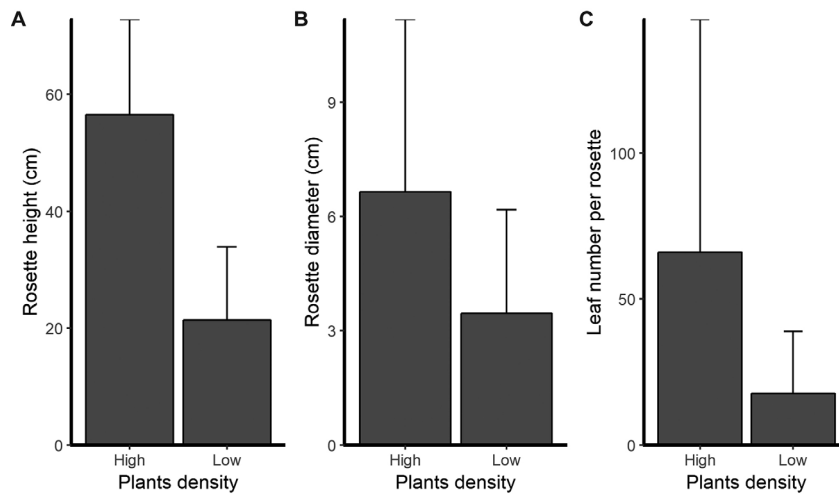
RESULTS

All measured variables presented higher mean values in the high-density condition. Rosette height ($t = 8.725$, $p < 0.05$, Fig. 3a), diameter ($t = 4.45$, $p < 0.05$, Fig. 3b), and number of leaves ($t = 4.71$, $p < 0.05$, Fig. 3c) were significantly higher on high-density conditions, allowing us to verify that plants were larger on high-density conditions.

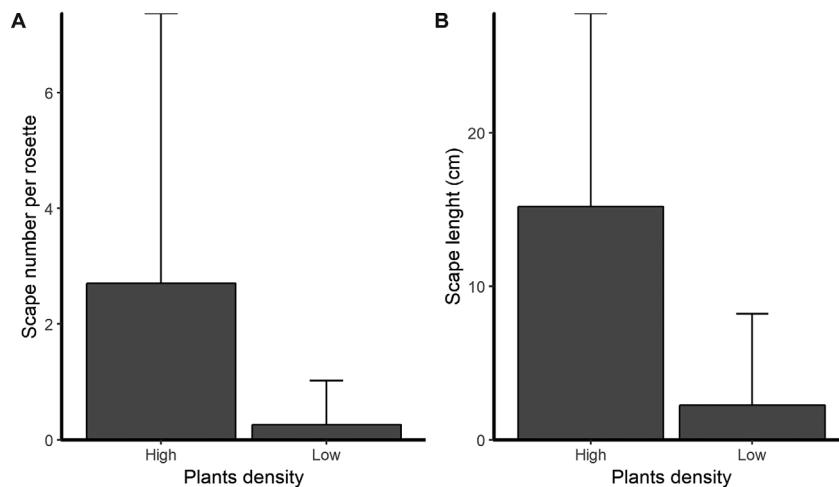
The reproductive structures also showed the same pattern of response. The flower number was higher in high-density conditions; plants on low-density conditions did not present any flower, despite the presence of some scapes. The number of flower scapes ($t = -6.2208$, $p < .0001$, Fig. 4a) and the maximum length of flower scapes were both also higher on high-density conditions ($t = 6.63$, $p < .05$) (Fig. 4b).



Figs. 2. A-B. A. A flowering specimen of *Vellozia albiflora* Pohl on gneiss outcrops of Morro do Cruzeiro, MG, Brazil. B. Sampling area showing a dense mat of plants, determined as the “high density” condition in this study. Bar = 3 cm.



Figs. 3 A-C. A. Rosettes height in centimeters in contrasting density conditions; B. Rosettes diameter in contrasting density conditions; C. Leaf number per rosette in contrasting density conditions. The bars represent the mean and the line is the standard deviation.



Figs. 4 A-B. A. Flower scape number per rosette in contrasting density conditions; B. Flower scape length in contrasting density conditions.

DISCUSSION

Regarding the influence of high density on vegetative morphological traits of *V. albiflora*, our results do not corroborate our hypothesis. The sampled rosettes presented larger sizes in high-density conditions, since both diameter and height presented higher values in densely crowded sampling units. Morphologic adaptations can arise in species under environmental pressures (Coelho *et al.* 2005; Alvarenga *et al.* 2013; Demetrio *et al.* 2014b). Since *V. albiflora* presents a rosette morphology (Mello-Silva 2009), greater diameters imply in more vigorous stalks. In shallow and sandy soils, common at rocky outcrops, a greater diameter would allow better fixation and sustentation for the plants (Sposito & Santos 2001), as it is common for other species that face uprooting (Demetrio *et al.* 2014b). In addition, in highly competitive habitats, plants may invest more biomass in traits that represent an advantage

on resource acquisition (Alvarenga *et al.* 2013, Coelho *et al.*, 2005), as *V. albiflora* showed by investing in larger plant sizes.

Another limiting factor in rocky outcrops is water availability (Madeira & Fernandes 1999; Coelho *et al.* 2008). *Vellozia* is known for use their leaves as foraging organs to obtain water (Oliveira *et al.* 2005). The number of leaves was higher in plants in high-density conditions what imply in a greater ability of water uptake from the surrounding atmosphere. Besides, bigger plants in high-density conditions probably experiment more favorable moisture conditions, since they form more closed “canopies”, generating a crowded mat over the soil, and by concentrating more leaves per area they may increase the area of shaded habitats.

In relation to reproductive traits, our results clearly confirm high density as a trigger for sexual reproductive enhancement (Abrahamsom 1975), since in high-density

conditions *V. albiflora* presented higher production of reproductive structures, here identified as the flower scapes that are directly involved in sexual reproduction, than in low-density conditions. Both number of flowers and number of scapes were higher in high-density conditions. In these conditions the formation of seeds can be considered as a persistence strategy, since seeds are persistence structures in other rocky outcrops as in *campos rupestres* (Garcia *et al.* 2007), due to the ability to remain in dormancy in the soil and germinate mainly under favorable condition, which is known for *Vellozia* species seeds (Garcia & Diniz 2003, Garcia *et al.* 2007, Mota & Garcia 2017). Even in resource-limited stressing habitats the high production of seeds in crowded conditions seems to be the best evolutionary strategy for clonal plants (Ikegami *et al.* 2012). In fact, a bigger body size, as that presented by *V. albiflora* in high-density conditions, may improve sexual reproduction, as noted for other plant species growing on rocky outcrops (Demetrio *et al.* 2014a).

Another strategy is the production of structures that can be dispersed and colonize other environments where resources are available or more abundant. Soils in rocky outcrops are usually shallow and poor (Negreiros *et al.* 2008), thus the existence of structures with persistence and dispersion functions in high densities are an optimal way of resource allocation for maximization of the fitness, granting higher possibilities of establishment and survival of new individuals.

Contrary to our hypothesis, the flower scapes length was higher in high-density conditions. At first, we thought that a higher energy limitation would decrease the investment in structures that are not directly linked to sexual reproduction. However, scapes have an important function on exposing flowers to pollinators. They can be considered as ancillary structures (Bazzaz *et al.* 1987), which are not directly involved on the processes that determine sexual reproduction but are imperative for the process functioning. This feature may represent a strategy to facilitate the dispersion to more favorable habitats with higher resource availability, what may represent an important evolutionary strategy in habitats where resources are distributed in patches, as rocky outcrops (Coelho *et al.* 2008, Negreiros *et al.* 2008) and show the importance of flower scapes in plant dispersion.

It is also possible that plants of *V. albiflora* allocated in densely crowded conditions presented higher number of flowers and greater flower scapes length because they also presented larger plant sizes. Body size is one of the most important factors regarding herbaceous perennial plant life-histories and several fitness components of these organisms are related to size (Méndez and Karlsson 2004), since it plays an important role on plants reproduction (Cheplick 2005, Demetrio *et al.* 2014).

Vellozia albiflora presented larger plant sizes and production of sexual structures in high-density conditions, what is counterintuitive in resource limited habitats as rocky outcrops. In this ecological framework we

would expect that plants under low-density conditions would be more able to explore and acquire resources, and so present larger plant sizes and higher number of sexual reproduction structures. However, the enhancing of growth under resource limitation conditions may represent an alternative to improve competitive ability, and a higher number of sexual reproductive structures may represent a way to scape from crowded conditions via seeds production (Abrahamsom 1975), generating higher chances of individual persistence and reproductive success. It is probable that these features are linked to persistence and survival of individuals allocated in low resources habitats like rocky outcrops. It is also possible to consider that high density conditions were responsible for generating more suitable microhabitat conditions, with higher soil moisture, caused by the existence of shaded habitats composed by the *V. albiflora* big individuals, and higher soil organic matter contents, caused by the plant leaves decomposition. We suggest that future works should investigate ecophysiology and reproductive success to verify how density affects the performance of *V. albiflora*.

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