Body size and clonality consequences for sexual reproduction in a perennial herb of Brazilian rupestrian grasslands

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Abstract

Body size is one of the most important factors regarding herbaceous perennial plants life-histories, and several fitness components of these organisms are related to size. Clonal plants show distinct kinds of reproduction and can develop offspring by sexual or asexual ways. We aimed to understand how body size affects *Comanthera nivea* (Eriocaulaceae) sexual reproduction and to verify how clonal growth is related to flower head production in this species. We sampled 600 rosettes in rupestrian grasslands and performed linear regression analysis between body size and number of produced flower heads. We also compared the flower head production between isolated rosettes and rosettes within clones. Our results showed that body size was significantly related, but explained only a small part of flower head production. The flower head production was higher in rosettes within clones than in isolated ones. The clones presented a rosette or a small group of rosettes that concentrated the sexual reproduction. Clonality was positively associated with sexual reproduction. Clonality can represent an important way of allowing the persistence of plants by sexual reproduction in markedly seasonal stressful environments. The cases of clonality enhancing the sexual reproduction must be considered and put in focus on reproductive biology research.

Keywords: body size, life history, clonality, reproductive strategies, sexual reproduction, Eriocaulaceae.

Consequências do tamanho de corpo e da clonalidade para a reprodução sexuada de uma herbácea perene doa campos rupestres brasileiros

Resumo

O tamanho de corpo é um dos atributos de história de vida mais importantes para plantas herbáceas perenes e muitos componentes da aptidão desses organismos são relacionados ao tamanho. As plantas clonais apresentam diferentes tipos de reprodução e podem gerar prole por vias sexuadas ou assexuadas. Nosso objetivo foi compreender como o tamanho de corpo afeta a reprodução sexual em *Comanthera nivea* e verificar como o crescimento clonal relaciona-se à produção de capítulos dessa espécie. Nós amostramos 600 rosetas em campos rupestres e utilizamos regressões lineares para verificar a relação entre o tamanho de corpo e o número de capítulos produzidos pela planta. Nós também comparamos a produção de capítulos entre rosetas isoladas e rosetas pertencentes a clones. Nossos resultados mostram que o tamanho de corpo tem influência positiva significativa na produção de capítulos, mas explica apenas parte da variação nos dados. A produção de capítulos é maior em rosetas pertencentes a clones que em rosetas isoladas. Os clones geralmente apresentam uma roseta, ou um grupo de rosetas, que concentra a reprodução sexual. A clonalidade apresentou ligações significativas com a reprodução sexuada. Em ambientes sazonais a clonalidade pode representar uma importante forma de persistência das plantas já que pode permitir um melhor desempenho da reprodução sexuada em vista dos estresses ambientais. Os casos nos quais a clonalidade representa uma via de melhor desempenho para a reprodução sexuada devem ser considerados e colocados em foco na pesquisa em biologia reprodutiva.

Palavras-chave: tamanho de corpo, história de vida, clonalidade, estratégias reprodutivas, reprodução sexuada, Eriocaulaceae.

1. Introduction

Body size is one of the most important factors regarding herbaceous perennial plants life-histories and several fitness components of these organisms are related to size (Méndez and Karlsson, 2004). It largely influences demography (Kirkpatrick, 1984) and also plays an important role on plant reproduction (Cheplick, 2005). Through growth plants become able to store resources and after use them to produce the necessary organs to sexual reproduction (Weiner et al., 2009). Clonal plants show distinct kinds of reproduction and can develop offspring by sexual or asexual ways (Fischer and van Kleunen, 2001; Pan and Price, 2001). Harper (1977) discriminated the individuals generated by seeds and those generated by meristematic development and named them genets and ramets, respectively.

Clonality can also improve the plant fitness since it may offer a connection between mother and daughter ramets (Roiloa et al., 2010). This connection is very important in rupestrian grasslands because it may enhance survival of ramets (Coelho et al., 2008a). These different life-histories may have evolved in response to environmental adversity (e.g. low availability of resources, water stress, soil erosion) (Gadgil and Solbrig, 1972; Rajakaruna et al., 2003; Guerrero-Campo et al., 2008). For the genus *Leiothrix* (Eriocaulaceae), Coelho et al. (2008a,b) showed the existence of species using both reproductive strategies to survive and persist in rupestrian grasslands, but there is no literature dealing with the effect of clonal growth on the investment on sexual reproduction for Eriocaulaceae species. This life history pattern may have arisen because the plants of this family had evolved in environments with strong abiotic selective pressures like shallow soils, seasonal lack of water on soil, and low nutritional conditions.

The rupestrian grasslands are an exclusive physiognomy of the Brazilian Cerrado, which is considered a global biodiversity hot spot (Myers et al., 2000; Marris, 2005). They occur in the highlands of Southeastern and in small disjunct locations of Northeastern Brazil (Negreiros et al., 2009). As proposed by life history theory (Stearns, 1992), in an environment with a limited amount of resources, like rupestrian grasslands, the resources should be used with the proposal of fitness maximisation. In the case of simultaneously sexual and asexual reproduction there should occur a balance between the two ways of reproduction. This balance would allow an optimal use of resources leading to the maintenance and persistence of the plant species. This work aims to understand how the body size affects *Comanthera nivea* (Bong.) L.R.Parra & Giul. (Eriocaulaceae) sexual reproduction, and to verify if clonal growth is related to flower head production in this species. Specifically we tried to answer the following questions: 1) Does the increase in body size cause an increase in the flower head production in both isolated rosettes and clones? 2) Will the number of produced flower heads be different between isolated rosettes and rosettes within clones? 3) Do the rosettes within clones present a similar number of flower heads when the clone is flowering or is there differential production among these rosettes?

2. Material and Methods

2.1 Study site

Rupestrian grasslands vegetation is constituted by an herbaceous layer, shrubs and sparse subshrubs (Alves and Kolbek, 2010). Plants frequently present imbricated leaves or rosette formation, occurring morphologic convergence among many families. Some of them occur in great areas like:Velloziaceae, Orchidaceae, Bromeliaceae, Melastomataceae and Eriocaulaceae (Giulietti and Menezes, 2000). Rupestrian grasslands can be also characterised by the association between vegetation, rock outcrops and sandy soils located at the high areas of the Mantiqueira mountain range (Benites et al., 2007). Soils with gravel texture, low nutrient availability and associated to rock outcrops are common on the Mantiqueira mountain range (Benites et al., 2007).

2.2 Study species

Comanthera individuals grow on rupestrian grasslands, associated with shallow, sandy or rocky soils, with low pH, especially in those soils generated by erosion of sandstones and quartzite. The highest number of species is found in rupestrian grasslands at the Espinhaço Mountain Range, in Minas Gerais and Bahia states, in Brazil. *Comanthera nivea* occurs exclusively in those rupestrian grasslands and have the leaves growing in a basal rosette. The flower head inflorescences are present. There can be formation of seeds, by sexual reproduction, although clonal growth by rhizomes and pseudovivipary can also occur (Parra et al., 2010).

2.3 Terminology

In general, clonal plants present offspring production by sexual and asexual ways. A genet is an individual formed through sexual reproduction by seed formation. The ramet, it should be noted, is defined as an individual formed by vegetative growth and is physiologically independent of its parental plant. In the case of *C. nivea* we found populations with isolated rosettes and also rosettes within clones. All of them were considered ramets since we could not identify which of them was formed by seed germination.

We considered the rosette (shoot forming) and its associated root system as a ramet. Hereafter we call all the ramets rosettes. When necessary the term individual is used as a synonym of all the sampled plants including isolated rosettes and clones.

2.4 Plant sampling

We settled four sampling quadrats of 1 m^2 each. The size of the quadrats was selected based on plant size. At the rupestrian grasslands of Serra da Bocaina *C. nivea* only occurred under stone slabs, in shaded habitats.

We marked 300 isolated rosettes and 300 clones with aluminium tags. For each isolated rosette we quantified the number of flower heads; for each clone we quantified the total number of produced flower heads, the number of rosettes within the clone and the number of flower heads produced per rosette. For the comparison of body size we used the basal area of the rosette or clone as an estimate.

2.5 Data analysis

To verify the influence of body size on *C. nivea* sexual reproduction we sorted 150 individuals of our initial sample. The sorted individuals included isolated rosettes and clones. Then we performed linear regression analysis between the individual area and produced flower heads number. We also compared *C. nivea* body size with literature data on body sizes of other Eriocaulaceae species.

To test the influence of clonal growth in sexual reproduction we compared the number of produced flower heads between isolated rosettes and rosettes within clones performing Mann Whitney U-tests. For each clone we sorted a rosette that was used in the comparison.

We also performed χ^2 tests to verify if the rosettes within clones presented equal or different flower head production frequency.

3. Results

The basal areas ranged from 0.2 cm² to 78.5 cm² for individuals of *C. nivea* and the mean basal area presented by the sampled individuals was of 13.31±0.56 cm², and 71% of the sampled individuals presented smaller basal areas than the mean. *Comanthera nivea* individuals with basal area below 0.6 cm² did not produce any flower head.

Plant area presented a significant and positive linear relation with flower head number ($r^2 = 0.24$; $p < 0.001$) (Figure 1). However, the amount of variation explained by this variable was small, indicating low relationship between body size and sexual reproduction in *C. nivea* (Figure 1).

Flower head production in rosettes within clones was significant higher than in isolated rosettes and the rosettes within clones presented a higher number of produced flower heads than the isolated ones. ($U = 68107.000$; $p < 0.001$) (Figure 2). The chi-square test showed a significant difference ($\chi^2_{(0.05)[1]} = 46.41$; $p < 0.001$) (Figure 3) between the frequency of equal and different reproduction per rosette within clones. In the sampled clones, 90 presented an equal number of flower heads per ramet and 210 presented different number of flower heads per ramet. In general one or a small group of rosettes inside the clones was responsible for sexual reproduction while the other rosettes belonging to the clone remained in their vegetative state.

4. Discussion

4.1 Influence of body size in sexual reproduction

Life history theory predicts that factors that decrease the probability of adult survivorship (e.g. low availability of resources) should also decrease the reproductive maturity (Stearns, 1992). Rupestrian grasslands are environments that show nutrient-poor soils and low water holding capacity (Negreiros et al., 2008). These features combined result in a stressful environmental condition that may constrain plant biological processes. According to resource allocation

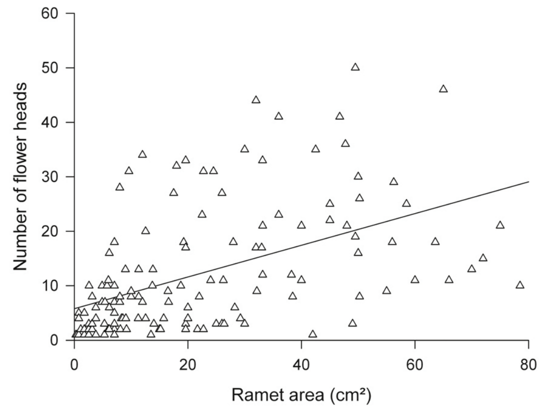

Figure 1. Linear regression between ramet area (cm²) and number of flower heads per ramet ($r^2 = 0.24$; $p < 0.001$; N=150). The line represent the equation $y = 0.291x + 5.77$.

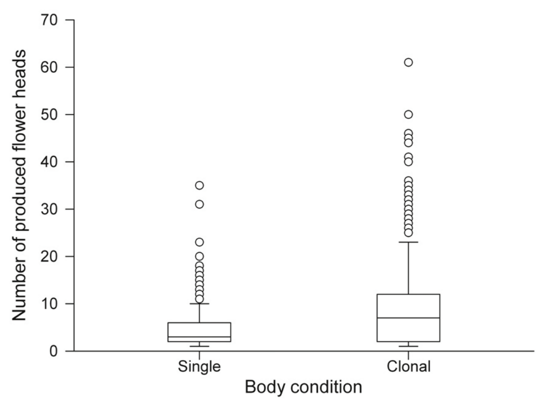

Figure 2. Box plot of the number of produced flower heads in clonal versus single ramets of *Comanthera nivea* ($U = 68107.000$; $p < 0.001$). The boxes represent the 25th and the 75th percentiles, the lines inside the boxes represent the median, the lines above and under the boxes represent the standard deviations, the circles represent outliers.

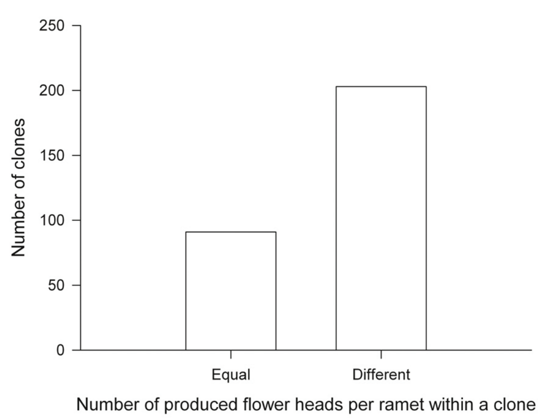

Figure 3. Number of cases of equal and differential reproduction among ramets in clonal individuals of *Comanthera nivea* ($\chi^2 = 46.41$; $p < 0.001$).

Table 1. Mean ± standard error (cm) diameters (MD) of rosettes of Eriocaulaceae species found in Southeastern Brazil rupestrian grasslands.

Species	MD
Leiothrix curvifolia	4.0 ± 0.3
L. crassifolia	4.3 ± 0.2
L. spiralis	3.7 ± 0.3
L. vivipara	2.5 ± 0.1
Comanthera nivea	2.5 ± 0.04

theory (Stearns, 1992), this limitation occurs because the amount of available resources should be partitioned for all the biological processes of the organism body. When submitted to these conditions plants should maximise their reproductive effort whereas optimal resource allocation is intended to lead to the increase of the organism fitness (Korfiatis and Stamou, 1999).

In comparison to *Leiothrix* (Eriocaulaceae) species *C. nivea* presented small body size, since its diameter was smaller than the smallest *Leiothrix* species recorded by Coelho et al. (2007) (Table 1). Although *C. nivea* individuals presented a mean basal area of 13.31±0.56 cm^2, the threshold size for reproduction was very small (about 0.6 cm^2 of basal area). This can be linked to environmental resource scarcity. Environmental conditions that limit growth (e.g. resource impoverishment) can favour the beginning of reproduction at small sizes (Bonser and Aarssen, 2009). It is suggested (Reznick, 1985) that the occurrence of trade-offs between traits linked to reproductive effort and growth would be more apparent in environments with nutrient limitation, however plants are clearly unable to reproduce without first reach some minimum vegetative size (Bonser and Aarssen, 2009). As *C. nivea* individuals reach sexual reproduction ability at small body sizes it is not necessary to remain allocating resources for growth. This small reproduction threshold size is what weakens the relation between body size and sexual reproductive for this species.

4.2 Influence of clonality in sexual reproduction

The relation between clonality and increase in sexual reproduction was strong in *C. nivea.* The rosettes within clones present higher flower head production than the isolated ones. Clonality is a well-documented reproductive mode for Eriocaulaceae. Coelho et al. (2008b) found clonal growth by rhizomes and pseudovivipary for the genus *Leiothrix*, and Gütschow-Bento et al. (2010) also verified clonal growth in *Syngonanthus*. The ability of producing clonal offspring may mean a way to facilitate growth and survival by improving the plant access to nutrients in environments that shows low supplies of resources (Hutchings and de Kroon, 1994; Alpert and Stuefer, 1997; Hutchings and Wijesinghe, 1997), and also in places where the resources are irregularly distributed (Seligman and Henkin, 2003). The connection and integration between the parental ramet and the daughter ones was considered a disadvantage in homogeneous environments, but is discussed as an advantage in environments that are highly heterogeneous (Alpert, 1999) as rupestrian grasslands (Coelho et al., 2008b; Negreiros et al., 2008). It also leads the ramet to inhabit large areas using its capacity to spread horizontally (Herben and Hara, 1997; Hutchings and Wijesinghe, 1997).

As a result of meristematic development, the ramets should present a genetic structure very similar to its parental plant and the clonal growth of *C. nivea* occurs in the phalanx mode (Lovett-Doust, 1981). Based on these facts and on the premise that flowering is controlled by genetic and environmental factors, we could expect that the flower head production per ramet would be equal or very similar since the clone has the same genetic structure and assess the same quantity of resources from the environment. Our results show, however, that the frequency of rosettes within the clones with differential flower head production is higher than the frequency of rosettes producing the same or a very similar number of flower heads. Based on this difference, and on the fact that clonal integration potentially allows division of labour in clonal plants (Alpert and Stuefer, 1997), on the strong physical and possibly physiological integration among the modules of plants using the phalanx strategy (Lovett-Doust and Lovett-Doust, 1982; Schmid and Bazzaz, 1991), and on the fact that the ramet morphology is highly influenced by the environmental variables (Ikegami et al., 2007) we suggest a division of labour among the ramets of *C. nivea*. Some of the ramets inside the clone are responsible for "foraging", absorbing nutrients and, afterwards, using the link and possibility of translocation between the ramets they send the photoassimilates to ramets responsible for flowering. These results suggest that clonality is an important trait for sexual reproduction to *C. nivea* and elucidates the relationship between the increasing of resource assimilation and sexual reproduction for clonal plants in seasonal stressful environments like the rupestrian grasslands.

Despite its importance, the body size explains only a small amount of the variation in the sexual reproduction of *Comanthera nivea*. Clonality, on the other hand, presented significant and important links with sexual reproduction. We conclude that in rupestrian grasslands clonality can represent an important way to amass the necessary resources for sexual reproduction in seasonal stressful environments. We also conclude that although many plants with clonal growth have suppressed their sexual reproduction during evolution, the cases of clonality enhancing sexual reproduction must be considered and focussed on in reproductive biology research.

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