Original Article

Soil factors effects on life history attributes of *Leiothrix spiralis and Leiothrix vivipara* (Eriocaulaceae) on rupestrian grasslands in Southeastern Brazil

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Abstract

In this study, we hypothesized that the life history traits of *Leiothrix spiralis* and *L. vivipara* would be linked to soil factors of the rupestrian grasslands and that rosette size would be influenced by soil moisture. Soil analyses were performed from five populations of *L. spiralis* and four populations of *L. vivipara*. In each area, three replicates were employed in 19 areas of occurrence of *Leiothrix* species, and we quantified the life history attributes. The microhabitats of these species show low favorability regarding to soil factors. During the dry season, their rosettes decreased in diameter due the loss of its most outlying leaves. The absence of seedlings indicated the low fecundity of both species. However, both species showed rapid population growth by pseudovivipary. Both *L. spiralis* and *L. vivipara* exhibit a kind of parental care that was quantified by the presence of connections between parental-rosettes and ramets. The findings of the present study show that the life history traits are linked to soil factors.

Keywords: life history, mountain habitats, pseudovivipary, soil factors; water scarcity.

Efeitos de fatores do solo nos atributos de história de vida de *Leiothrix spiralis* e *Leiothrix vivipara* (Eriocaulaceae) nos campos rupestres no Sudeste do Brasil.

Resumo

Neste estudo, testamos a hipótese de que os traços da história de vida de *Leiothrix spiralis* e *L.vivipara* estariam ligados a fatores do solo dos campos rupestres, e que o tamanho de roseta seria influenciado pela umidade do solo. As análises de solo foram realizadas a partir de cinco populações de *L. spiralis* e quatro populações de *L. vivipara*. Em cada área, três repetições foram empregadas em 19 áreas de ocorrência das espécies de *Leiothrix*, e quantificamos os atributos de história de vida. Os microhabitats destas espécies apresentam baixa "favorabilidade" em relação aos fatores de solo. Durante a estação seca, as rosetas diminuíram de diâmetro devido à perda de suas folhas mais periféricas. A ausência de plântulas indicou a baixa fecundidade de ambas as espécies. No entanto, ambas as espécies apresentaram crescimento rápido da população por pseudoviviparidade. Tanto *L. spiralis* quanto *L. vivipara* exibem um tipo de cuidado parental que foi quantificada pela presença de conexões entre rosetas parentais e rametes. Os resultados do presente estudo mostram que os traços da história de vida estão ligados aos fatores do solo.

Palavras-chave: história de vida, habitats de montanhas, pseudoviviparidade, fatores do solo, escassez de água.

1. Introduction

Life history theory seeks to explain the evolution of traits that are closely related to fitness, such as body size, age at first reproduction, number of breeding episodes, fecundity and life span (Stearns, 1992). An organism's life history may be looked upon as resultant of three biological processes, namely, maintenance, growth, and reproduction. Any organism has limited resources of time and energy at its disposal. The three component processes of the life history compete for these limited resources (Gadgil and Bossert, 1970). Life histories are the result of an optimal allocation of resources or energy among maintenance, growth and reproduction (Demetrius, 1975). It has also been shown that life history strategies may evolve in response to environmental adversity (e.g. low availability of resources) (Rajakaruna et al., 2003). Southwood (1977, p. 360), concluded that, "the multitude of ecological strategies that we observe in nature arise from the evolutionary trade-offs of costs versus benefits in the process of adaptation to habitats".

Traits like long length of life, late maturity, low fecundity, low rate of increase, and favorableness of pseudovivipary (analogous to parthenogenesis for animals) are related to harsh environments (Braby, 2002). All these features combined has been described as stress tolerance by Grime (Grime, 1977), in which selection favors traits that support retention and conservative use of acquired mineral nutrients (Warembourg and Estelrich, 2001). In this study, we will attempt to connect life history traits of two plant species, *Leiothrix spiralis* and *L. vivipara*, with their habitat characteristics, specifically analyzing the soil factors. Therefore in rupestrian grasslands there is a great limitation for nutrients (Coelho et al., 2008a; Negreiros et al., 2009). We employ a soil chemical classification to evaluate the habitat favorability as low, medium and high. These species are pseudoviviparous and endemic from rupestrian grasslands in Southeastern Brazil (Coelho et al., 2005). A unique and rare vegetation physiognomy of the Brazilian Cerrado, a biodiversity hotspot (Myers et al., 2000; Marris, 2005), known as the rupestrian grasslands, is exclusively found in the highlands of the Espinhaço mountain range and small disjunctions in southeastern and northeastern Brazil (Negreiros et al., 2009). Rupestrian grassland is comprised of exposed rocks and sand. They comprise a mosaic of edaphic habitats formed at one extreme by quartz gravel-derived soils, and at the other extreme by sandstone-derived soils on the top of mountains (Giulietti et al., 2000). Rupestrian grassland is a harsh environment for plants, it has a predominance of shallow and sandy soils with low fertility and low water-holding (Ribeiro and Fernandes, 2000). The extremely low fertility status of these soils conditioned the development of survival strategies by the vegetation, involving physiological and morphological adaptations (Benites et al., 2007). The main attribute that plant species adapted to environments with low resource availability must have is an inherent low growth rate, even when exposed to optimal levels of resources (Rajakaruna et al., 2003). These species allocate fewer resources to growth because a higher level of supply is needed to functions that increase survival rates in adverse environments (Arendt, 1997) and so, in these rock outcrop habitats, clonal growth, specifically pseudovivipary, is important in the maintenance of *L. spiralis* and *L. vivipara* populations (Coelho et al., 2006).

Based on the following premises: (1) water is the main limiting resource in arid and semi-arid ecosystems (Pendleton and Meyer, 2004), as well as in rupestrian grasslands , (2) reproductive modes in *Leiothrix* are microenvironment-related, specifically to soil conditions (Coelho et al., 2008a) and that (3) *L. spiralis* and *L. vivipara* are not relatively related in a phylogenetic overview (Giulietti et al., 1995) we hypothesized that the life history traits of these two species would be linked to soil nutrients and moisture and that the body size would be determined mainly by soil moisture.

2. Material and Methods

2.1. Study site

The fieldwork was accomplished at Serra do Cipó National Park. Plants were not collected; all the measures of the plants were accomplished in field, with the permission of the direction of the Serra do Cipó National Park.

The Serra do Cipó is located in the southern portion of the Espinhaço mountain range in the state of Minas Gerais, Brazil, between 19°12'–19°20'S and 40°30'–43°40'W and altitudes varying from 1000 to.1100 m. The climate is considered mesothermic, with mild summers and a rainy period during the summer, and the temperatures vary from 17 to 20° C. The annual precipitation in the region is nearly 1500 mm; there is a dry period during the winter, which lasts 6-7 months (April to September), and a moist period which lasts 5-6 months (October to March). Rupestrian grasslands occur on quartzite and sandstone outcrops, which form sandy and shallow soils. It has the greatest extension and complexity in the Espinhaço Mountains; it is dominant above 1000 m. They are the result of the quartzite erosion, forming plain areas with shallow, nutrient poor soils, with poor organic matter content (Medina and Fernandes, 2007). Due to their shallow depths, most of soils associated with rock outcrops are classified as "Neossolos Litólicos" in the Brazilian Soil Classification System, which correspond to the Entisol order of the US Soil Taxonomy and to the Leptosols of the FAO soil classification system (FAO, 1998; EMBRAPA, 1999).

The vegetation of Serra do Cipó is diverse, comprised mainly of rupestrian grasslands. It has a continuous herbaceous layer with sparse shrubs. Poaceae, Cyperaceae, Velloziaceae, Xyridaceae and Eriocaulaceae are quite common in the region (Giulietti et al., 2000) and all form rosettes. The Eriocaulaceae family is well represented, with several endemic taxa in this formation (Ramos et al., 2005). *Leothrix spiralis* individuals were located at points around 19°15'33" S and 43°31'42" W; and those of *L. vivipara* at 19°17'12" S and 43°35'13" W. In both locations, the

Braz. J. Biol., 2014, vol. 74, no. 4, p. 828-836

829

soil is sandy, shallow, acid, nutrient-poor, and becomes more compact in dry periods.

2.2. Study species

Leiothrix individuals grow in rosettes from which scapes with flower-head type inflorescences appear (Giulietti et al., 1995). The scapes in pseudoviviparous species function like stolons when the flower heads of rosettes proliferate, giving rise to plantlets (Coelho et al., 2005). Most of the species show both sexual reproduction and clonal growth. Seed production is rare in *L. spiralis* and *L. vivipara* (Giulietti et al., 1995). In *L. vivipara* in particular there is a reduction in the number of flowers per flower head and the majority of the central portion of the flower head is occupied by leaves (Giulietti et al., 1995). In *L. spiralis*, field observations have been unable to detect seedlings of sexual origin and it is thought that population regeneration occurs mainly through clonal propagation corresponding to the splitter-ramet strategy (Coelho et al., 2006). Low seedling recruitment in pseudoviviparous taxa is common in habitats with unfavorable conditions for seed germination and establishment (Lee and Harmer, 1980; Bauert, 1993; Miao et al., 1998). *Leiothrix vivipara* occurs in dry, sandy soil, sometimes densely covered by an herbaceous layer. Most plantlets remain supported by the scapes or are intertwined with herbaceous leaves. Coelho et al. (2005) recorded only one attached plantlet for each 100 supported plantlets in sites crowded by herbaceous plants. The flower heads of the suspended plantlets also proliferate giving rise to new plantlets. This process may repeat itself several times. Thus, *L. vivpara* is a pseudoviviparous canopy-forming species (Coelho et al., 2008b). In *L. spiralis*, the plantlets are formed late, only after the flower heads touch the ground. A few rosettes grow amongst herbaceous plants, even if these are sparse. In addition, practically all the plantlets formed are attached to the ground (Coelho et al., 2005).

2.3. Plant sampling

It is common to find rosettes of *L. vivipara* in densely crowded conditions, which makes it difficult to obtain demographic data. Therefore, for this species, we sampled 50 clones with 59 rooted rosettes and 281 suspended rosettes in a 1.2 m² plot. For *L. spiralis*, we sampled 100 clones with 120 rosettes. However, due to their rosette dispersion it was necessary to establish two 1m² plots, containing 50 clones in each. All rosettes were marked with numbered aluminum tags, so they could be followed monthly during the two rainy seasons from December 2003 to December 2004. However, for *L. vivipara* the measurements were obtained until October 2004, since in November a fire occurred in the region close to the *L. vivipara* population, and destroyed most of the rosettes. For each individual plant of both species, we quantified the following life history attributes: (1) size of rosettes; (2) growth of rosettes; (3) fecundity (see below). For measures of size, 100 rosettes of *L. vivipara* and 130 rosettes of *L. spiralis* were randomly marked, besides those in the

permanent plots. We compared the measured life history traits: body size, maturity, rate of increase of population, fecundity and parental care with the habitat characteristics, in an attempt to draw links between soil factors and life history traits. Rate of increase of population was measured by the number of pseudoviviparous ramets and number of seedlings (originated from seeds). This numbers were obtained at the end of the rainy season, according to the procedure adopted by Coelho et al. (2007). Fecundity was quantified by seedlings number originated of seeds, since we attempted to verify the link between life histpry traits and soil factors in a demographic perspective. Pseudoviviparous reproduction efficiency was quantified by transformation ratios from flower heads in ramets. Parental care was quantified as a binary variable, noting the presence/absence of a connection between parental-rosette and ramets at least during a single ramet life period.

2.4. Soil sampling

Soil samples were collected using a borer of 5 cm diameter and 10 cm depth from five populations each of *L. spiralis* and four populations of *L. vivipara*. The roots of these taxa are small and fine, thus rooting depth corresponds to the soil sampling depth. In each of the areas, three replicates were employed and a total of 81 soil samples were obtained in 19 areas of occurrence of *Leiothrix* species. Analyses of the chemistry, texture and content of organic matter were conducted for each soil sample. The pH was determined potentiometrically in water, $CaCl_2$ and KCl solution (1: 2.5). The concentration of hydrogen and aluminium ions was determined by titration with NaOH, and extraction made Ca $(OAc)_2$ (0.5 mol/l, pH 7.0). The sum of exchangeable bases (SB = Σ K + Ca^{2+} + Mg^{2+} $cmol_c/dm^3$), base saturation (V = Σ bases x 100/ CEC (capacity of cationic exchange) $cmol_c/dm^3$), P (mg/ dm^3), aluminium saturation (m = 100 x Al^{3+}/ CEC) were determined. The content of organic matter was expressed as a percentage (OM = %C x 1.72). The classification of the soil factors as low, medium and high was made in agreement with the commission for fertility of the soil of the State of Minas Gerais, (Ribeiro et al., 1999). The percentage of coarse sand, thin sand, silt and clay were combined in a single variable denominated "texture" = (silt % + clay %)/(coarse sand % + thin sand %). The texture variable expresses the relative water-holding and nutrients capacities. This measurement seems to be more appropriate in sandy or gravel and shallow soils, since the percent moisture can provide a seasonal measure related to the rainy or dry season. Low and high soil moistures were defined as the lowest and the highest soil moistures found during the study period.

2.5. Data analysis

To verify the efficiency of pseudoviviparous reproduction we performed reference curves (y = x) by linear regression analysis. Probability flowering was performed using logistic regression by equation: of reproduction = $e^{(\beta_s + \beta\ diameter)}$/ 1 $+e^{(\beta_s + \beta\ diameter)}$. To test the effect of soil water availability

830

Braz. J. Biol., 2014, vol. 74, no. 4, p. 828-836

we compare the body size of *L. spiralis* and *L. vivipara* at low and high soil moisture using a Mann-Whitney U-test (Sokal and Rohlf, 1981).

3. Results

The measured soil factors as well as the favorableness of the habitat classification (low, medium and high) are showed in Table 1. Analyzing the soil data and life history traits of *L. spiralis* and *L. vivipara* we found potential linkages between the habitat characteristics and the life history strategies of the two studied species, expressed by the observed maintenance of fitness attributes (growth, reproduction and survival).

Both *L. spiralis* and *L. vivipara* showed rapid population growth. Although no seedling has been found, many ramets were formed. The initial population of *L. spiralis* (100 rosettes in December 2003) increased by 67 rosettes, all by pseudovivipary, until December 2004. In *L. vivipara*,

the growth was higher, the initial population with 50 rosettes in December 2003, reached 105 fixed rosettes in October 2003, also all by pseudovivipary. The absence of seedlings indicated the low fecundity of both species and the proportion of flower heads originating ramets showed a higher clonal growth potential for both species (0.92) for *L. vivipara* and (0.48) for *L. spiralis,* indicating the efficiency of pseudoviviparous reproduction mode. These transformation ratios from flower heads in ramets can be seen through the reference curves y = x. The regression curve in *L. vivipara* is almost equal to the reference curve y = x (Figure 1b). Points belonging to the curve y=x indicate that all of the flower heads produced ramets. In *L. spiralis*, the regression curve is situated under the reference curve (Figure 1a). Points under the regression curve indicate that of those flower heads produced few originated ramets.

Both *L. spiralis* and *L. vivipara* exhibit a kind of parental care that was quantified by the presence of connections between parental-rosettes and ramets. The fact that none

Table 1. Habitat classification of *Leiothrix spiralis* and *L. vivipara* as for the favourability, mediated by soil factors.

Soil variables	L. spiralis	L. vivipara	Habitat favourability (chemical classification)
pH	4.289 ± 0.074	4.100 ± 0.070	Low (larger acidity)
H + Al ($cmol_c$ dm^{-3})	9.132 ± 1.392	9.057 ± 2.450	Low (larger potential acidity)
P (mg dm^{-3})	1.371 ± 0.071	1.791 ± 0.182	Low (dystrophic soils)
SB ($cmol_c$ dm^{-3})	0.363 ± 0.052	0.309 ± 0.075	Low (dystrophic soils)
m (%)	76.794 ± 2.750	83.528 ± 1.939	Low (larger indexes of aluminium saturation)
V (%)	4.485 ± 0.549	4.487 ± 0.451	Low (dystrophic soils)
OM (dag Kg^{-1})	3.667 ± 0.316	3.609 ± 0.582	Medium (reasonable availability of nutrients for plant)
N (dag Kg^{-1})	0.179 ± 0.013	0.174 ± 0.025	Low (dystrophic soils)
Texture (%)	0.083 ± 0.006	0.107 ± 0.015	Low (lower water-holding capacity)
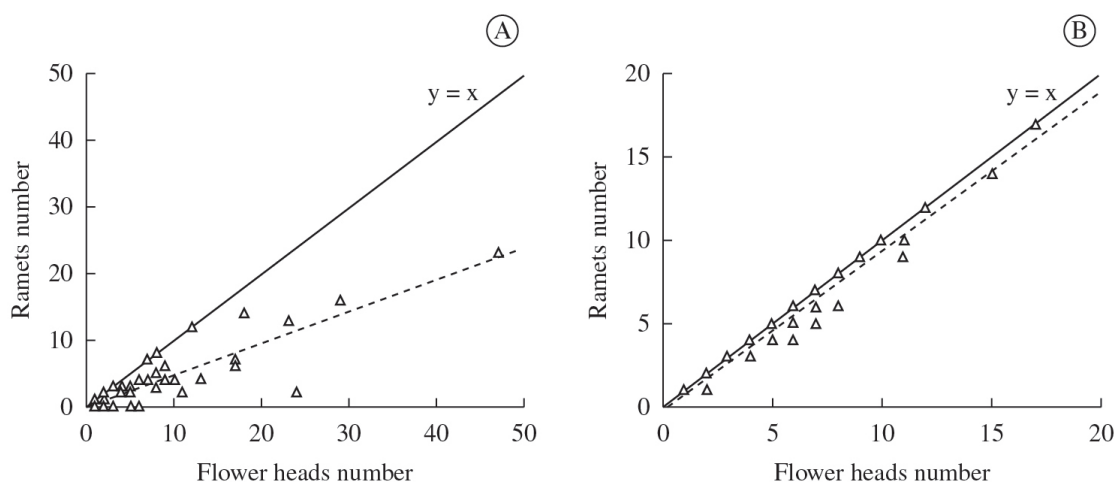
Figure 1. Ramets produced by pseudovivipary. A) *L. spiralis*- Points belonging to the curve y=x indicate that all of the flower heads produced were transformed into ramets. Note that the majority of the points are over the curve y=x indicating that most of the flower heads were transformed into ramets. The stipple line represents the regression curve y = 0.97x − 0.28; r² = 0.97; p < 0.001; n = 40. B) *L. vivipara*- Note that most of the points are under this curve. The stipple lines represent the regression curve y = 0.76x − 0.051; r² = 0.97; p < 0.001; n = 50.

Braz. J. Biol., 2014, vol. 74, no. 4, p. 828-836

831

of the ramets died while connected to the parental plant indicates the importance of parental care. The connections in *L. vivipara* are more durable than those of *L. spiralis*. Duration is at least 11 months for *L. vivipara*, but they can remain up to 2 years (F. F. Coelho, personal observation). In *L. spiralis*, the connections are maintained only during the first 4-5 months of the ramet life. After scapes split, ramets survival depended on the ramet size. All ramets with less than 0.5 cm died soon after the severing of the connections.

Flowering in both *Leiothrix* species appeared linked to plant size. In *L. vivipara* all rosettes flowered as soon as they reached the minimum size, i.e., 0.5 cm (Figure 2b). While for *L. spiralis*, rosettes less than 1cm in diameter did not produce any inflorescences (Figure 2a), that can be described by the sigmoid function: Probability of

reproduction = $e^{(-6.723 + 2.340\ \text{diameter})}/\ 1 + e^{(-6.723 + 2.340\ \text{diameter})}$, McFadden's Rho-Squared = 0.55.

The soil moisture affects *L. spiralis* and *L. vivipara* body size and the rosettes exhibited great variation in growth. In fact, for both species, few rosettes grew during the study period; with most of them decreasing in diameter. In *L. spiralis* 54 (n = 100) rosettes grew in size, 11 (n = 100) remained with the same diameter and 29 (n = 100) decreased in diameter (Figure 3a). Four of the 100 rosettes measured initially died. In *L. vivipara*, only four (n = 50) rosettes grew (four point above the curve y = x) and all the others decreased in diameter (Figure 3b). Of 50 rooted rosettes, 11 died. The decrease in diameter occurred because, during the dry season, the rosettes lost most outlying leaves. The rosettes were significantly smaller in low soil moisture for *L. vivipara*
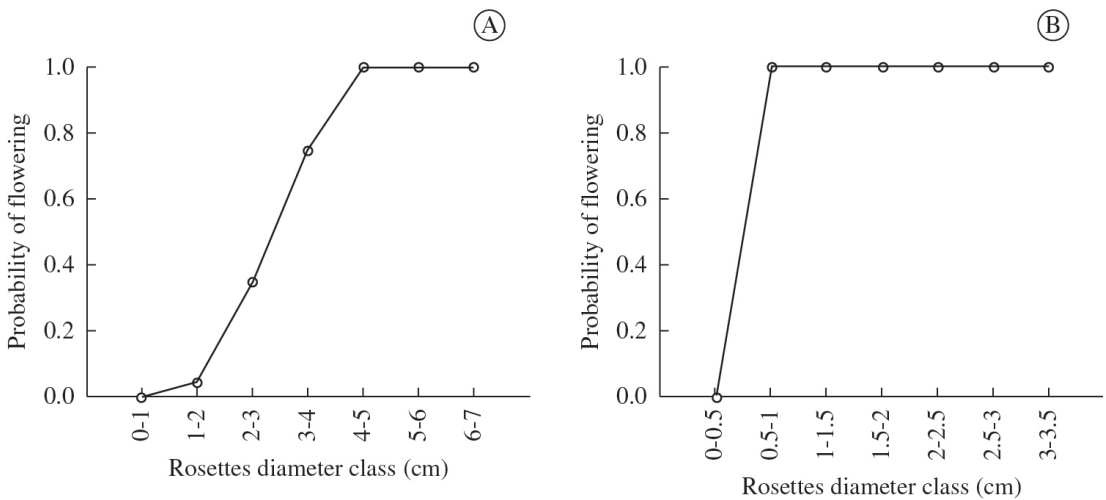

Figure 2. A) Probability of flower heads production as a function of rosette diameter in *L. spiralis* and B) in *L. vivipara*.
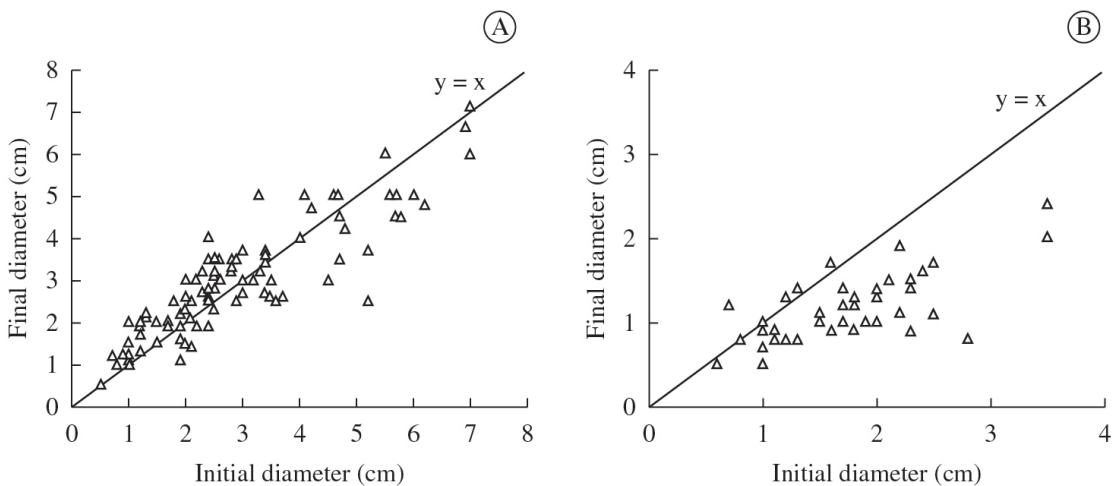

Figure 3. Final diameter as a function of rosettes initial diameter. A) *L. spiralis*- Points along the curve y = x indicate unaltered diameter during the 13 month period. Points above the curve indicate growth and under indicate diameter decrease. B) *L. vivipara*- The few points along the curve y = x indicate unaltered diameter in the 11 month period and over indicate growth. Note that most of the points are situated under the curve indicating diameter decrease.

832

Braz. J. Biol., 2014, vol. 74, no. 4, p. 828-836

(U test = 585.000, p < 0.001) (Figure 4a). However, did not affect the body size of *L. spiralis* (U test = 5202.500, p = 0,615) (Figure 4b).

4. Discussion

Many studies have concluded that patterns in species traits are significantly related to environmental conditions where these species occurred (Van Kleef et al., 2006).

Leiothrix spiralis and *L. vivipara* are both characterized by having a small body size in relation to other *Leiothrix* species (Coelho et al., 2007), early reproduction and rapid population increase. All these attributes can be associated with temporary and unpredictable habitats. However, these species show differences in the frequency of vegetative and reproductive events. In *L. vivipara*, ramet production occurs throughout the year, while *L. spiralis* reproduces only once during the year (Coelho et al., 2006). Repeated reproduction (or iteroparity/ polycarpy) is a characteristic associated to predictable environments, while reproduction synchronized with favorable periods can be related both to permanent and temporary habitats.

Both species showed slow growth of rosettes and low fecundity, attributes considered as components related to harsh environments (Grime, 1977; Braby, 2002). During the dry season, the rosettes loose most of their outlying leaves, with only the central leaves remaining green. This effect suggests that the rupestrian grasslands impose physiological constraints on these plants, indicating that the resource allocation for growth is absent during this period. Thus, all available resources can be allocated to pseudoviviparous reproduction. Clonal growth, specifically the pseudovivipary, is important to the maintenance of *L. spiralis* and *L. vivipara* populations (Coelho et al., 2006). Pseudovivipary is an asexual reproductive strategy,

in which vegetative propagules are produced instead of sexual reproductive structures (Elmqvist and Cox, 1996). By contrast, vivipary is a sexual reproduction process in which seeds germinate within the fruit with subsequent embryo development before the seeds are dispersed from the parent plant (Elmqvist and Cox, 1996).

Analogous to parthenogenesis, which has been cited as being selected under environmental stress pressure (Greenslade, 1983), the pseudovivipary reproductive mode of both species can also be considered as an attribute resulting from harsh environment conditions, since it occurs very frequently in strongly seasonal environments such as arid, semi-arid, arctic or alpine environments (Sarapul'tsev, 2001). Pseudovivipary has been correlated with the ability to grow in dry soils (Salisbury, 1942). In arctic and alpine grasses, such as *Festuca*, *Deschampsia*, *Poa* and *Polygonum*, pseudovivipary represents a mechanism that leads to survival and maintenance of populations in these extreme environments characterized by short growing seasons (Chiapella, 2000; Sarapul'tsev, 2001). Both *L. spiralis* and *L. vivipara* grow in dry, nutrient poor and sandy soils. In areas formed by dry and sandy soils, sexual reproduction becomes unfavorable because the substrate is very harsh for seed germination and seedlings establishment (Scarano, 2002). Coelho et al. (2006) suggested that pseudovivipary also represents a mechanism that contributes to the survival and maintenance of *L. spiralis* and *L. vivipara* populations. The success of pseudovivipary in these environments relies on the parental care provided by the parental plant to the offspring until their establishment. Vegetative propagules have the advantage of staying connected to the parental-plant, at least during the first stages of their lives. This increases their survival probability in environments with extreme conditions because the integration among ramets promotes the flow of photoassimilates between the parental
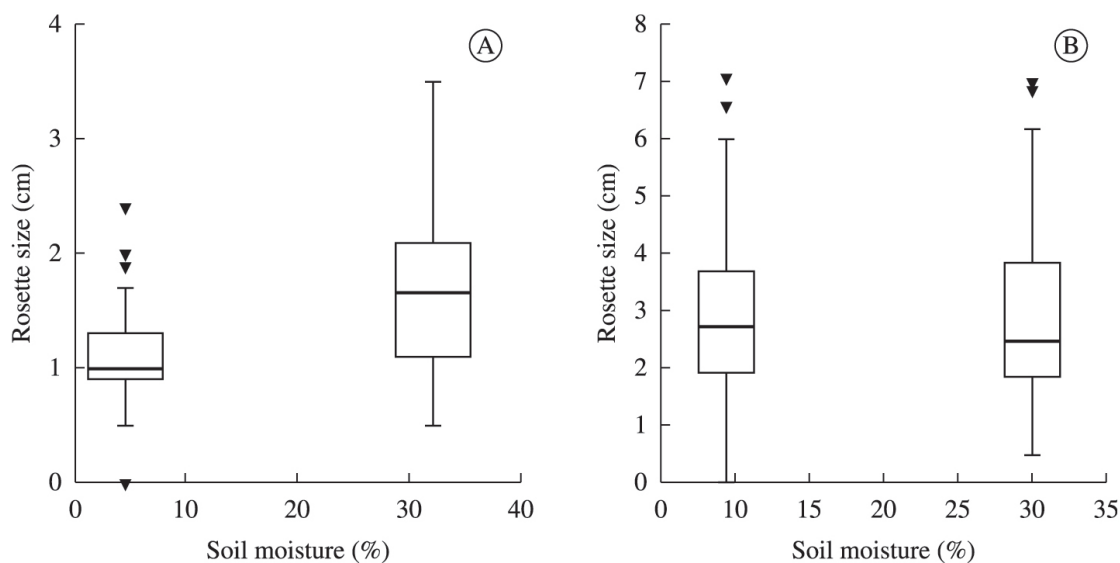
Figure 4. Body sizes during the high and low soil moisture seasons. A) *L. vivipara* body sizes differences between the dry and moist seasons. B) *L. spiralis* body sizes differences between the dry and moist seasons.

ramet and the daughter plant (Marshall, 1990). Moreover, the pseudovivipary has been considered one of the most efficient modes for numerical increase of ramets (Grace, 1993). Therefore, in spite of the slow growth of rosettes, the population can experience a rapid numerical increase in ramets (Coelho et al., 2008b).

Rupestrian grasslands are not as unfavorable as arid, arctic or alpine environments, but it soils are nutrient-poor and have low water holding capacity (Ribeiro and Fernandes, 2000), but nevertheless possess a considerable diversity of species. Predictability refers to temporal availability of resource (nutrients and water), which in turn is regulated by summer rainfall. Rainfall in the winter occurs only occasionally. Environmental unpredictability is related mainly with the transition period between seasons.

Life history strategies represent different solutions to particular ecological problems, thus providing a connection between individual species traits and environmental conditions. These species evolved biological properties compatible with their persistence in their natural environment. Acquiring characters that made possible the minimum reduction of fitness, even in conditions judged as not favorable for plant establishment. In comparison, plants which do not show attributes like reduction of body size and pseudovivipary could present reduction on its adaptive success when put on habitats with worse conditions in view of its natural ones, as happened to *Iris* in a common garden transplant experiment (Dorman et al., 2009).

Regarding to rosette negative growth the depletion of soil moisture was the main determinant for the shorter body size at the end of dry season. According to the resource allocation theory and with the fact that defoliation is related to changes in resources availability and environmental changes, like variation on soil moisture, during the year (Vaughton and Ramsey, 1998) we could predict that this decrease on growth rates would turn available the most part of acquired resources to the survival of the individual. Feng and Li (2007) found that soil moisture was the most important factor related to the number of leaves and biomass allocation on *Amomum villosum*, showing a very significative correlation between these life history traits and soil moisture. This result could be linked to ours in the sense of a clearly indication that the reduction of body size by negative growth in *L. spiralis* and *L. vivipara* is a response mechanism to the water stress providing chances for survival until the next moist season. The decrease on body size can also be related to the fact that populations growing on environments where water is seasonally available has high allocation to reproductive structure as showed by Van Kleunen (2007) in a greenhouse experiment. The low soil moisture did not affect the body size of *L. spiralis*. That can be due to the fact of the rhizome presence in this species, what may allow the resources storage during the moisture season and posterior consumption during the dry season, what would turn *L. spiralis* able to show a smaller defoliation. *Leiothrix. vivipara* showed great negative growth behavior due its probable inability of stocking resources since structures like rhizomes are lacking in this species.

Our results showed that *L. spiralis* and *L. vivipara* reach the early maturity, because the flowering occurred after 0, 5 and 1 cm respectively. This may represent an attempt of early reproduction since Coelho et al. (2007) found that the average diameter for these species are 3.7±0.3 cm and 2,5±0.1 cm. According to Hall and Willis (2006) and Franks et al. (2007) the selection may favor early flowering in habitats where water availability decreases over the growing season.

Departing from our theoretical foundation that the characteristics of *L. spiralis* and *L. vivipara* described in this study are typical from stressing habitats and from the findings of the present study concerning to soil factors, we corroborate the hypothesis that the life history traits of these two species are linked to soil nutrients and moisture and that the body size are determined mainly by soil moisture.

Acknowledgements

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835

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836

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