

## Clonal growth and dispersal potential of *Leiothrix flagellaris* Ruhland (Eriocaulaceae) in the rocky grasslands of Southeastern Brazil

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(received: September 8, 2004; accepted: January 16, 2007)

**ABSTRACT** – (Clonal growth and dispersal potential of *Leiothrix flagellaris* Ruhland (Eriocaulaceae) in the rocky grasslands of Southeastern Brazil). *Leiothrix flagellaris* is a small clonal plant that grows in sandy/rocky, nutrient poor soils in the rocky grasslands (“campos rupestres”) of southeastern Brazil. In the rainy season most of their flower heads differentiate into small rosettes, produced by pseudovivipary, and connected to the mother-plant by flexible, elongated stalks that can reach up to 90cm. Most of these rosettes remain suspended over rocks or over the sparse herbaceous surrounding vegetation, while a few arch low enough to come into contact with the surrounding soil and take root. These suspended rosettes can reach diameters comparable to currently rooted and reproductively active rosettes produced during previous reproductive periods. As the rooted rosettes grow up, their potential to generate and disperse new pseudoviviparous rosettes increase rapidly. This unusual guerrilla strategy of *L. flagellaris* seems to congregate a suit of traits that promote a fast increase in photosynthetic area and improve recruitment, thereby helping to circumvent dispersal and establishment failures in its severe environment.

Key words - canopy development, clonal reproduction, demography, dispersal, pseudovivipary

**RESUMO** – (Crescimento clonal e potencial de dispersão de *Leiothrix flagellaris* Ruhland (Eriocaulaceae) em campos rupestres do Sudeste do Brasil). *Leiothrix flagellaris* é uma pequena planta clonal que se desenvolve em solos arenosos/pedregosos e pobres em nutrientes dos campos rupestres do sudeste do Brasil. Durante a estação chuvosa, a maioria dos seus capítulos se transforma em rosetas geradas por pseudoviviparidade e que são ligadas à planta-mãe por hastes flexíveis que continuam seu crescimento e alcançam até cerca de 90cm. A maioria destas rosetas permanece suspensa sobre pedras ou sobre a rala vegetação herbácea local, enquanto que uma pequena fração toca o solo e se enraíza. Estas rosetas suspensas alcançam tamanhos comparáveis ao de rosetas enraizadas e produzidas nas estações reprodutivas precedentes e que já se reproduzem. À medida que as rosetas enraizadas crescem, seu potencial de gerar e dispersar novas rosetas pseudovivíparas aumenta rapidamente. A estratégia de crescimento guerrilha de *L. flagellaris* parece reunir características que permitem rápido incremento da área fotossintética e elevam as chances de recrutamento, provavelmente reduzindo insucessos na dispersão e estabelecimento em seu severo ambiente.

Palavras-chave - demografia, dispersão, formação de copa, pseudoviviparidade, reprodução clonal

### Introduction

Clonal reproduction in plants may be described as an extension of the individual's ability for indeterminate modular growth that duplicates the whole individual without the need for sexual reproduction (Tiffney & Niklas 1985). The asexual recruit, or ramet, produced in this way is a modular unity of clonal growth that can potentially exist independent of the parent plant (conversely, the genet is a genetic individual, product of a zygote) (Harper 1977). The production of ramets may compensate for seedling recruitment failures (Seligman & Henkin 2000, Arizaga & Ezcurra 2002), reducing

the mortality risks of the genet by spreading the risk among an assembly of ramets, with potentially independent life (Cook 1985, Eriksson 1993). The ability to ‘move about’ by virtue of rhizomes, stolons or rooting shoots allow clonal plants to form large clonal stands, of exploiting patchy habitats by jumping over barriers of unsuitable substrates, or insinuating themselves through a dense matrix of taller plants (Crawley 1997). This is allowed because when a clonal plant spreads, the connections linking the old established individual to the new recruited ramets may enhance temporally their maintenance, growth and/or survival under unsuitable environmental conditions (Hartnett & Bazzaz 1983, Cook 1985, Peltzer 2002). This integration may be especially beneficial in environments where resources are scarce and/or patchily distributed both in time and space, such as sand dunes or rocky ground (Pitelka & Ashmun 1985, Alpert & Mooney 1986), since resources can be re-distributed within the clone from sites of acquisition to sites where resources are scarce (Hutchings 1988, Hutchings & Wijesinghe 1997). Thus,

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clonality increases stress-resistance in the bromeliads *Aechmea nudicaulis* (L.) Griseb. and *Vriesea neoglutinosa* Mez that colonize the patchy resource-poor coastal plain environments of southeastern Brazil (Sampaio *et al.* 2002). On the other hand, the large *A. nudicaulis* ramet system creates settlement opportunities to other less-stress resistant plant species (Sampaio *et al.* 2005), highlighting the importance of clonal integration even to such ecosystem processes (see Scarano 2002).

Two general strategies of clonal reproduction are evident in terrestrial plants. The non-linked strategy typifies bulbils and seeds generated by agamospermy, whereas the linked strategy is found in plants that spread by stolons or rhizomes (Tiffney & Niklas 1985). For plants using the linked strategy, the branching of daughter ramets within the clone may be interpreted as a form of foraging when there is plasticity in internode length and branching frequency (Bell 1984). This may be achieved by two extreme growth forms: 1) “phalanx”, in which the genet expands as a broad front, developing tightly packed modules close enough to overlap their resource depletion zones; and 2) “guerrilla”, which minimizes the overlap in resource depletion zones, due to the large spacing of modules (Lovett Doust & Lovett Doust 1982, Harper 1985). A phylogenetic analysis of 2300 clonal plants from Europe indicates that phalanx is more associated to open, dry, nutrient poor environments, while guerrilla is associated to wet, shady, nutrient rich environments (van Groenendael *et al.* 1996).

The rocky grasslands (“campos rupestres”) of the Espinhaço Mountain Chain are the center of genetic diversity of plants within the South American genus *Leiothrix* (Eriocaulaceae) (Giulietti & Hensold 1990). In some species of this genus, center-apical meristems from the flower heads differentiate into a small caulinar axis containing leaves and roots, after the production of seeds (Monteiro *et al.* 1976, F. Vale unpublished data). Connected to the mother-plant by long stalks, these rosettes eventually touch the soil and then root (Monteiro *et al.* 1976). This type of clonal reproduction is known as pseudovivipary, a condition where vegetative propagules differentiate in some or all normal sexual flowers in the inflorescence (Grace 1993, Elmqvist & Cox 1996). The revision made by Elmqvist & Cox (1996) points to rarity of pseudovivipary: it was described for approximately 50 species of angiosperms belonging to families such as the Agavaceae, Alliaceae, Liliaceae, Poaceae, Polygoneaceae and Saxifragaceae. The Eriocaulaceae family was not cited in this revision (Coelho *et al.* 2005).

In this study we describe the pseudoviviparous reproductive strategy of *L. flagellaris* Ruhland on a gravel, dry, open, and nutrient-poor environment. Despite a general

lack of natural history information concerning aspects of sexual reproduction and population ecology of this species, and the fact that our study was restricted to one sampling season, we could address the following questions: a) how does the production and potential dispersal of the ramets vary with rosette diameter?; b) what is the potential contribution of this clonal reproductive mode to population growth?; and c) does soil texture influence the chances of ramet rooting and spreading?

## Material and methods

**Study area** – The rocky grasslands comprise an extremely diverse community of grasses, herbs, and scattered shrubs, dominating the dry, shallow, sandy and/or gravel, nutrient-poor soils on the mountain tops of the Espinhaço Mountain Chain, Brazil (Giulietti *et al.* 1987, Rizzini 1997, Giulietti & Menezes 2000). The study was conducted in the “Parque Municipal Ribeirão do Campo” (19°03'–19°07' S and 37°31'–37°37' W), a preservation area which has around 3,150 ha, with altitude between 650 and 1,500 m (“Prefeitura Municipal de Conceição do Mato Dentro” 1999). The mean annual temperature of the region is 21 °C and mean rainfall around 1,500 mm. The dry (May–September, with rainfall around 124 mm) and rainy seasons are well defined (source: “Instituto Nacional de Meteorologia/Belo Horizonte”). We made three short field trips for field observations and data collecting. Most data regarding demographic and morphometric relationships were collected at the beginning of the rainy season of 2001 (from September 25<sup>th</sup> to the 30<sup>th</sup>); probability of ramet rooting was estimated at the end of the rainy season of 2004 (June 26<sup>th</sup>).

**Study species** – *Leiothrix flagellaris* was studied on a hilltop of about 900 m altitude (figure 1). The soil patch where the plants occurred was predominantly sandy or gravel, covered with sparse tussocks of grasses, a single species of Velloziaceae and a few other herbaceous plants. The rosettes of *L. flagellaris* can reach 11 cm in diameter. Very few were connected to other rosettes by rhizomes. Each rosette produces flower heads, that may contain seeds, and differentiate into small rosettes (ramets) that may be dispersed tens of centimeters from the mother-plant by very long stalks, which can attain up to 70 cm (figures 2–4). Some *Leiothrix* species from the “campos rupestres” (as *L. spiralis* (Bong.) Ruhland, *L. curvifolia* var *lanuginosa* (Bong.) Ruhland, *L. curvifolia* var *mucronata* (Bong.) Giul., and *L. crassifolia* (Bong.) Ruhland) reproduce during the rainy season (Coelho 2005). Therefore we suppose that the reproductive event observed in *L. flagellaris* could have started in the previous rainy season. However, in *L. vivipara* (Bong.) Ruhland the production of flower heads and pseudoviviparous rosettes is spread throughout the year. Besides, these pseudoviviparous rosettes can remain unrooted and connected to their mother rosettes by stalks for more than 2 years (F. Coelho unpublished data). Thus, we cannot discard

the possibility of having observed the cumulative product of more than one reproductive event in *L. flagellaris*.

**Developmental stages** – The sampled rosettes were classified according to three easily distinguishable developmental stages: (I) young immature, (II) old immature, and (III) old reproductive. The young immature stage was comprised of rosettes produced during the studied reproductive event, and connected to their mother rosettes by new functional stalks. Some were beginning to root, whereas most of these rosettes were suspended above the soil level, sometimes held by the surrounding vegetation. The old immature and old reproductive rosettes were produced in previous reproductive seasons. Most of them were still connected to their mother rosettes by old stalks (field experiments are necessary to determinate if they remain functional), while others were not connected (in this case, some of these rosettes could have been originated from seeds). All old immature and reproductive rosettes were rooted.

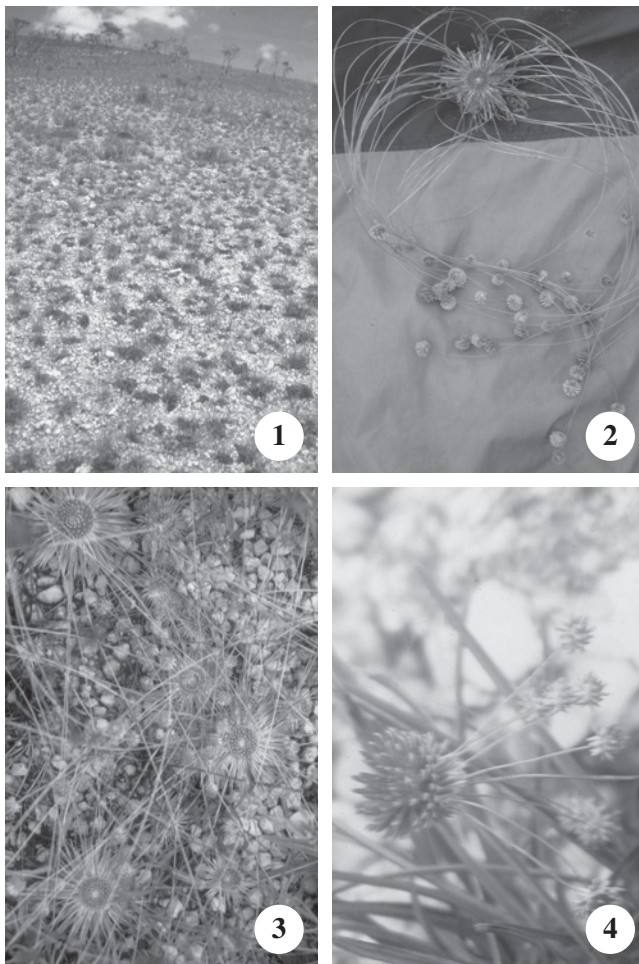


Figure 1. View of the hillside patch of white gravel soil where *Leiothrix flagellaris* occur. Notice the sparse herbs and grass tussocks. 2. A clone showing the dry leaves surrounding the rosette center and the long stalks supporting the young immature (diameter of the mother plant about 10 cm). 3. Clones growing on gravel soil. 4. Detail of a very rare event: a suspended young immature supporting new young immatures.

**Changes in population structure due to clonal growth** – Changes in population structure due to clonal growth were evaluated in 2001 from a sample of 749 rosettes measured along a transect, positioned in the gravel soil patch. We discriminated young immature from the old immature and reproductive rosettes. Rosettes were grouped in 1.0 cm diameter classes.

**Reproductive probability** – The sample of 749 rosettes was used to test whether probability of reproduction depended on rosette diameter. We estimated the diameter-related chances of reproduction: ratio between old reproductive to old immature plus old reproductive rosettes, grouped in 1.0 cm diameter classes. We adjusted a sigmoid curve, using the Gauss-Newton method, relating reproductive probability to rosette diameter. This was due to the existence of a minimum diameter for reproduction to occur, beyond which there is a sharp increase in the probability of reproduction up to 100%.

**Production and maximum dispersal potential of ramets** – The number of young immature rosettes produced and the maximum dispersal potential were estimated for 24 reproductive rosettes, sampled to cover the whole range of observed rosette diameters. We measured the rosette diameter and counted the number of young immature produced. We also measured the length of the longest stalk connecting the young immature to the mother rosette. The relationships between number of young immature and length of the longest stalks, and diameter of the mother rosette, were determined through linear regressions. **Growth and potential spreading of ramets** – We measured the rosette diameters and the length of their stalks in 7 reproductive rosettes that had produced from 4 to 116 young immature. We tested whether the diameter of those rosettes and stalks were correlated within the genets, by using Spearman's rank correlation.

**Soil type and ramet rooting** – To test whether the rooting distance depended on soil texture, during one-hour two persons searched for young immature rooted and measured rooting distances in the gravel, while a single person did the same in the sandy soil, along random transects. Rooting distances were measured for 59 rooting ramets belonging to different plants found in the sandy soil, whereas 51 were measured in the gravel. The average rooting distances in both soils were compared by Mann-Whitney test. Notwithstanding differences in *L. flagellaris* density and differences in search efficiency among the three persons, sample sizes obtained during the same searching time indicated the comparative difficulty of ramets rooting in gravel as compared to sandy soil.

**Probability of ramet rooting** – At the end of the rainy season of 2005 we estimated the chances of young immature rooting ( $n = 593$ , out of 110 clones) along a transect in the sandy soil. Spearman's rank correlation was used to test whether the number of rooted ramets increased with the number of ramets/clone. Probability of rooting was defined as the ratio between the number of rooted ramets/total of ramets/clone (suspended plus rooted).

All the statistical analyses were done using the program SYSTAT (Wilkinson 1989).

## Results

*L. flagellaris* clones – Each clone of *L. flagellaris* consists of a mother-rosette connected by stalks to a small population of pseudoviviparous ramets, most of them suspended above the soil and some rooted. Although in some clones at least three generations of rooted rosettes connected to each other by old stalks have been found, the stalk connections are not permanent. The stalks become dark with time, and eventually break. The death of mother-rosettes can cause the death of their suspended ramets. Notwithstanding, we have also observed ramets that remained alive while their mother rosette appeared dead. In this case, two situations were noticed: a) the mother rosette was unconnected and b) the mother rosette was connected to other rooted rosettes.

Population structure – As a result of the reproductive event of 2001 (and possibly, also, to prior reproductive events) the population structure acquired a “reversed-J shape” (figure 5). This was due to the incoming of new ramets ( $n = 295$ ), most of them unrooted and supported by the surrounding vegetation. Young immature were present in the first two diameter classes. From the first diameter class and on, old immature became progressively more infrequent, being substituted by reproductive rosettes.

Many of the rooted rosettes smaller than 2 cm in diameter were probably generated in the previous reproductive episode, as suggested by their small diameter and old stalks. These two diameter classes can potentially have their numbers elevated in a short time period, once

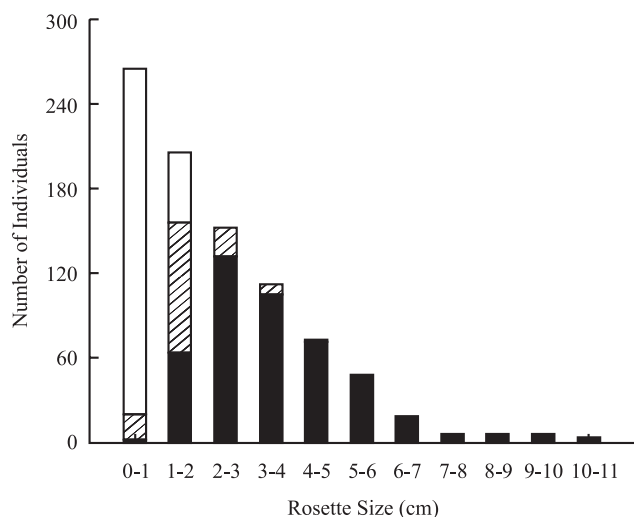


Figure 5. Population structure of *Leiothrix flagellaris* during the reproductive event: old reproductive rosettes (black bars), old immature rosettes (hatched bars), and young immature (open bars). Notice that the young immature were not reproducing, although they were in the same diameter classes in which reproduction is beginning to occur in older rosettes.

the young immature succeed in rooting. None of the young immature, some already rooted, were reproducing, although the old rooted rosettes of the same diameter were already capable of reproduction (figure 5).

Reproductive probability – In 2001, rosettes with diameter  $\leq 1$  cm rarely reproduced. From this diameter class on, the probability of reproduction increased quickly, becoming 100% in rosettes measuring more than 5 cm in diameter (figure 6A). This can be described by the sigmoid function:

$$\text{Probability of reproduction} = 100 [1 - e^{-(1.4 \text{ diameter})}]^{6.3}, r^2 = 0.99, n = 10.$$

Growth of ramets and stalks – The old reproductive rosettes produced from a few to tens of flower heads, most of them differentiated into young immature generally connected by stalks of different lengths (figure 2). This seems to occur early, as flower heads from stalks about 4 cm long were already differentiating into young immature. Larger young immature observed in 2001 were generally associated with longer stalks, suggesting correlated growth. This was partially confirmed by our small sample: young immature diameter and stalk length were positively correlated in the two larger clones ( $\geq 19$  young immature) ( $r_s = 0.58$  and  $r_s = 0.45$ ,  $P < 0.05$ , figure 6B), but not in the other 5 small clones ( $\leq 13$  young immature), in spite of some positive correlations ( $-0.55 < r_s < 0.33$ ,  $P > 0.05$ ). Production of ramets and maximum dispersion potential – Larger rosettes produced more ramets than the small ones (regression excluding the two possible stressed clones – white dots of figure 6C: number of ramets = 6.5 diameter – 15.2,  $r^2 = 0.88$ ,  $n = 22$ ,  $P < 0.001$ ). While they grow, the reproductive rosettes can spread their ramets to increasingly longer distances (stalk length = 5.1 diameter + 14.1,  $r^2 = 0.52$ ,  $n = 24$ ,  $P < 0.001$ ; figure 6D). The shortest stalk measured 3 cm and the longest one 70 cm in the measured plants, but 90 cm stalks were also observed.

Soil type and ramet rooting – The distances of ramet rooting are generally shorter than the length of their stalks. The rooting distances of the young immature stage were greater in sandy soil than in gravel (figure 7A, 7B). In sandy soil, the modal distance was 20-25 cm, while in gravel it was 5-10 cm ( $U = 503.5$ ,  $P < 0.001$ ,  $df = 1$ ). The shortest observed distance in sandy soil was 5 cm, and in gravel 3.3 cm, while the largest distance was 45 cm in both soil types, corresponding to about 50%-75% of the length of the largest stalks. Based on differences in sampling effort (two persons vs. one person finding similar number of rooted rosettes during the same searching time), it is possible to infer that in sandy soil the chance of rooting is about twice as great as in gravel.

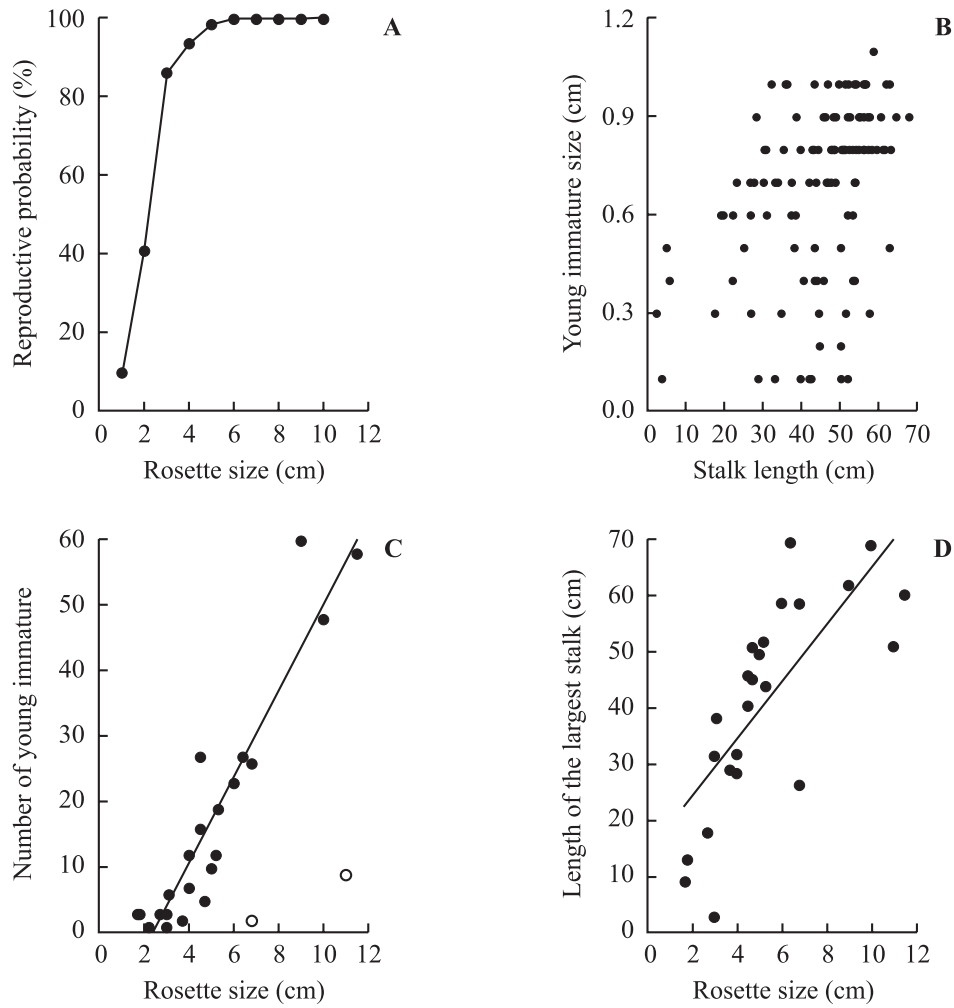


Figure 6. A. Relationship between probability of reproduction and rosette diameter in *Leiothrix flagellaris*. B. Diameter and stalk length of 116 young immature produced by a single reproductive rosette, suggesting that growth and dispersion of young immature occur jointly. C. Larger rosettes produce more young immature. D. Larger rosettes may be potentially dispersed to greater distances, due to their longer stalks.

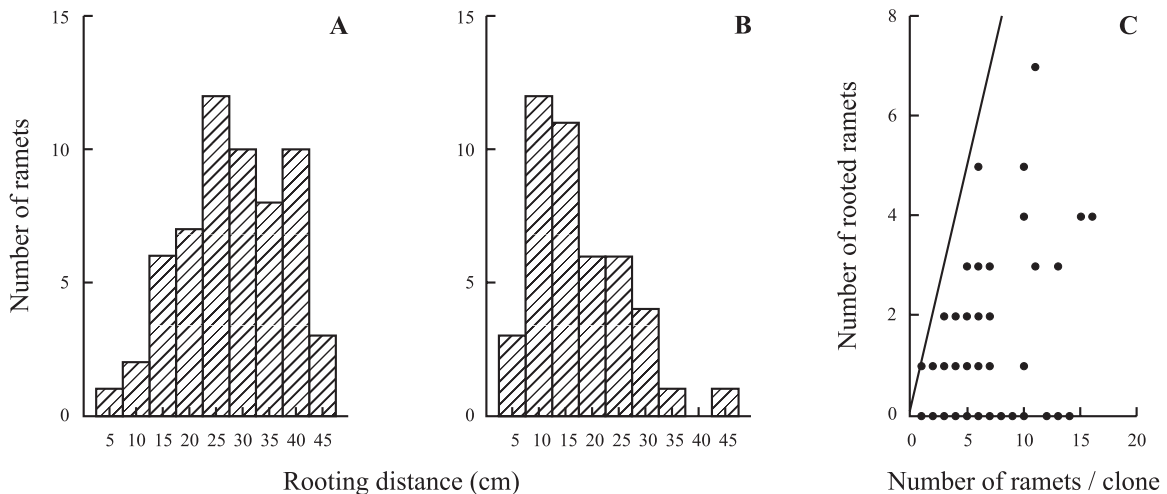


Figure 7. Distribution of rooting distances of *Leiothrix flagellaris* ramets on sandy soil (A) and gravel soil (B). C. The number of rooted ramets increases with clone ( $r_s = 0.30$ ,  $P < 0.01$ ,  $n = 110$ ). Points under the reference line ( $Y = X$ ) points to the commonness of unsuccessful rootings.

The number of ramets rooting in sandy soil, at the end of the rainy season of 2004, increased with the number of ramets produced by old reproductive rosettes (figure 7C). However, these chances are small: the proportion of young immature rooted was only 14% (83 rooted and 510 suspended ramets).

### Discussion

Pseudovivipary has been described for about fifty species of flowering plants. These are mostly found in arctic, alpine, or arid habitats, where the probability of an offspring to be dispersed in time or space to a patch better than the parental patch is very low. This feature reduces the advantages of seed dormancy or seed dispersal (Elmqvist & Cox 1996), thus success in such environments relies on the parental care provided by the mother-plant to the offspring until establishment (Richards 1986). The patch occupied by the population of *L. flagellaris* has a low richness and density of other plant species, indicating rigorous restrictions to establishment and/or survival. In addition to the hilltop location (where leaching is severe and infiltrating rainwater probably disappears first), the soil is sandy and/or gravel and the plants are exposed to high solar radiation and/or winds. Isolated or in combination, these factors may subject these hilltop plants to nutritional and hydric stress.

The clonal growth of *L. flagellaris* probably starts during the rainy season, when both young immature and seedlings will probably have greater survivorship and/or establishment chances. It seems to be an effective strategy for rapid increase in photosynthetic area, reproduction and ramet spreading, which altogether enhance chances of survival. This species seems to combine the main pseudoviviparous strategies observed in two other *Leiothrix* species: *L. vivipara* (development of a “canopy of ramets”) and *L. spiralis* (production and dispersion of ramets) (see Coelho *et al.* 2005). The small and numerous flower heads of *L. flagellaris* differentiate early in their development into small photosynthetic ramets that are spread around the mother-plant by long and flexible stalks. This contrasts with non-pseudoviviparous species of the genus, as *L. curvifolia* and *L. crassifolia*, in which short (< 10 cm), less flexible stalks keep the flower heads elevated above the mother rosettes (Coelho 2005). As the stalk elongates, the mother-rosette provides water and nutrients to the small ramet, for its maintenance and growth before and probably some time after rooting. However, many young immature are suspended and seem to be pushed over the sparse local vegetation. This is composed mainly of small Velloziaceae, grasses, and a

broad mesh formed by hundreds of *L. flagellaris* stalks, and reduces the chances of rooting of the young immature. The suspended ramets kept alive, although connected to dry rosettes, indicates that even after the death of the aerial portion of one of the members of the clone, their roots and stalks still allow the flux of water, carbohydrates and nutrients among the remaining members, suggesting a high level of physiological integration. Therefore, physiological integration allows a clone to even out spatial heterogeneity, and may benefit the clone as a whole (Silvertown & Doust 1993). A high risk of resource shortage combined with dispersal barriers imposed by clusters of bad sites can exert a sufficiently strong selection pressure for integration to become advantageous (Mágori *et al.* 2003).

Probably many young immature root soon after touching the soil for the first time. However, there is a possibility of some being pushed to the soil surface, before rooting, by the growing stalks (which would be more effective while the stalks are still short, due to their higher rigidity). Although stalk lengths were not measured, in gravel soil the rooting distances seems to be shorter, probably because of the greater number of obstacles blocking ramet movement. This probably also reduces the chances of ramet rooting, decreasing the ratio of rooted to suspended ramets, as compared to sandy soils. As the hanging young immature plants do not show developed roots, root growth is probably induced soon after soil contact.

In a habitat where resources are distributed in patches, the capacity to detect gradients of nutrients, produce roots, and establish shoots may greatly increase the success of the clone (Cook 1983). Considering the difficulties for rooting, what advantage would be associated to the precocious differentiation of *L. flagellaris* flower heads into young immature, while stalks are still very short? This strategy possibly increases chances of young immature rooting, especially in gravel soils, where narrow sandy patches alternate with gravel surfaces. Along the whole growth period of stalks, the young immature would have several chances to touch the soil and then root. Another possible advantage associated to the long stalks of *L. flagellaris* is that they might represent a demographic benefit of dispersal, placing offspring well away from the parent, which would be advantageous when resources are patchily distributed (see van Groenendael *et al.* 1996).

Although several of the *L. flagellaris* young immature belonged to size classes in which reproduction is almost imminent or even possible for rosettes, none of them (either suspended or rooting) were reproducing. This suggests that: a) the mother-rosette inhibits, at least for a while,

young immature reproduction; b) the young immature plants have the diameter but not the appropriate physiological age to reproduce; and/or c) some environmental stimulus is necessary for young immature reproduction to occur. However, it can be supposed that soon after establishment such young immature will be able to reproduce. The possible advantages of precocious reproduction, as opposed to late reproduction, for population growth are known: organisms that mature earlier may have higher fitness because their offspring are born earlier and start reproducing sooner (Stearns 1993). During development the chances of *L. flagellaris* reproduction and the number of produced young immature increased with rosette diameter. Since these plants experience several reproductive events during their lifetime, each genet has the potential to propagate many times within the population. Nevertheless, in *L. flagellaris* young immature production seems mainly associated to a fast increase in the photosynthetic area, since most of the ramets do not root. The genet will be composed of a young immature population, photosynthesizing and/or acquiring resources from the soil at different distances from the mother-rosette. This guerrilla-type expansion strategy, as found for *L. flagellaris*, is associated with fast habitat occupancy (Harper 1985), and low resource supply (Hutchings 1988).

Many *L. flagellaris* young immature do not succeed in rooting and must be temporarily nourished, imposing costs to the mother-rosette (if on the one hand the young immature are photosynthetic units, on the other they are points of water expenditure). Water loss may be critical during the dry season, due to a combination of high winds, high temperatures and dry sandy/gravel soils where this species occurs. While connected, the young immature can be supported by the mother-plant, while seedlings would be more prone to environmental hazards.

Although some results of this study should be interpreted cautiously (because they were obtained through static sampling), they indicate that *L. flagellaris* has an odd suit of demographic traits that enhance fitness in the hostile rupestrian field environment. In this species it seems to occur an environmentally-induced division of labor also verified in other clonal plants, in which the ramets can specialize functionally in the performance of different tasks such as resource uptake from above vs below-ground sources, vegetative spread and sexual reproduction (Stuefer 1998). The differentiation of flower heads into rosettes represent the profit of these reproductive structures that otherwise would be lost after senescence. The early maturation of established rosettes and the increased potential for clonal proliferation during growth suggest the importance of this strategy to the species. Furthermore,

the early development of the young immature connected to long growing stalks probably enhances their chances of rooting. Traits such as those are predicted to characterize clonal plants associated to resource-poor environments, subjected to disturbances that may damage or kill offsprings (such as drought) and spatial variation in favorable sites (see Grace 1993).

Acknowledgments – We would like to thank the City Hall of Conceição do Mato Dentro, especially its Environment Secretary Luiz Claudio Ferreira de Oliveira, for the lodging and food supplied during field work; Junio D. de Souza, Christina D.L. Capelo and Ana C. Neves, for help in field work; Fábio R. Scarano, Sérgio P. Ribeiro, Carlos A.K. Miranda and anonymous reviewers for their suggestions and critical review; Fernando Vale for clarifying the anatomy of pseudoviviparous rosettes.

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