Reproductive Modes in Leiothrix (Eriocaulaceae) in South-eastern Brazil: The Role of Microenvironmental Heterogeneity

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INTRODUCTION

Divergent natural selection associated with different habitats or ecological niches is increasingly viewed as the primary cause of speciation in plants (Lexer et al., 2003). For most flowering plant lineages, changes in the ecological attributes of populations, especially involving habitat and resource utilization, are an important component of speciation (Schluter, 2001; Levin, 2003). In continental floras, ecological speciation, i.e. the evolution of new species as a result of divergent selection on traits among populations in contrasting environments, is most apparent in regions with large numbers of endemics (Levin, 2003, 2004). Ecological speciation can generate evolutionary radiation in response to ecological opportunities (e.g. new microenvironments) (Ellis et al., 2006; Friar et al., 2006). Adaptive radiations are generally characterized by the accumulation of substantial morphological and ecological diversity within rapidly speciating lineages (Schluter, 1996). Such radiations appear to have played a central role in the proliferation of ‘stone plants’ in the genus Argyroderma (Aizoaceae) in the Cape Floristic Province in South Africa (Ellis et al., 2006). The role of microhabitat differences, especially substrate types such as sandstone and granite (Verboom et al., 2004) and quartz gravel soil (Ellis et al., 2006), on life history divergence and evolutionary radiation was investigated for Ehrharta (Poaceae) and Argyroderma, respectively, in the Cape region of South Africa. These studies show a direct effect of varied edaphic microhabitat on the adaptive radiation in these genera. Ellis and Weis (2006) suggested that the coexistence of Argyroderma species is facilitated by the response to fine-scale habitat variation. It has been shown that seedling distribution may correlate with microspatial variation in leaf cover and that species respond differently to the components of small-scale environmental heterogeneity in grassland habitat (Silvertown and Dickie, 1980; Silvertown and Wilkin, 1983). At small spatial scales (centimetres), rupetrian grasslands exhibit high heterogeneity in environmental factors such as vegetation cover conditions and soil factors.

Rupetrian grasslands show peculiar characteristics of soil and topography that provide wide environmental...
heterogeneity and promote a variety of microhabitats. These microhabitats favoured the diversification and endemism of many flowering plant families (Giulietti et al., 2000). Among flowering plants of rupestrian grasslands in Brazil that show a high level of endemism and richness, the Eriocaulaceae stand out (Ramos et al., 2005). The Eriocaulaceae comprises approx. 1200 species in ten genera. They have pantropical distribution, although the majority of the species occur in the mountainous regions of Venezuela and Brazil (Giulietti and Hensold, 1990). In these regions, they grow on sandy soils and rocky outcrops of quartzite and sandstone (Giulietti and Hensold, 1990). On these soils there is great variation in the vegetation cover, suggesting considerable scope for the diversification of reproductive modes in \textit{Leiothrix}.

The genus \textit{Leiothrix} is restricted to South America and contains 37 taxa (Giulietti and Hensold, 1990). \textit{Leiothrix flavescens} occurs in Brazil, Venezuela, Guyana and Peru, \textit{L. celiae} is exclusive to Venezuela, and the remaining taxa are endemic to small mountainous areas in the Brazilian states of Minas Gerais and Bahia (Giulietti et al., 1995). The highest species richness of \textit{Leiothrix} is concentrated in the mountains of Minas Gerais, where 25 taxa occur, 19 of them in the Serra do Cipó (Giulietti and Hensold, 1990).

Recently, data were presented showing a diversification on pseudoviviparous reproduction in two \textit{Leiothrix} species (Coelho et al., 2006). Of the 19 \textit{Leiothrix} taxa that occur at the Serra do Cipó, five have widespread spatial distribution. These five \textit{Leiothrix} taxa: \textit{L. curvifolia ‘lanuginosa’}, \textit{L. curvifolia ‘mucronata’}, \textit{L. crassifolia}, \textit{L. spiralis}, \textit{L. vivipara} and \textit{L. sinuosa} were selected. Moreover, these five taxa exhibit all possible reproductive modes found in the genus. Based on the observation that rupestrian sympatric species of \textit{Leiothrix} often differ in vegetation cover and edaphic conditions, the species were expected to show differences in microenvironment-related reproductive modes. Thus, in the present study, the micro-environmental heterogeneity is proposed to be an important reproductive mode-generating factor in \textit{Leiothrix}.

\section*{Materials and Methods}

\textit{Study area}

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, and a moist period which lasts 5–6 months. The rupestrian grasslands of the Serra do Cipó comprise a mosaic of edaphic habitats formed at one extreme by quartz gravel-derived soils, and at the other extreme by sandstone-derived soils. Rupestrian grassland has a predominance of shallow and sandy soils with low fertility and low water-holding capacity (Ribeiro and Fernandes, 2000). In these rock outcrop habitats, clonal growth, specifically pseudovivipary, is important in the maintenance of \textit{L. spiralis} and \textit{L. vivipara} populations (Coelho et al., 2006).

The vegetation of the Serra do Cipó is diverse, comprising mainly rupestrian grasslands. It has a continuous herbaceous layer with sparse shrubs. The rosette shape is a morphological convergence occurring in various families of herbaceous plants (Menezes and Giulietti, 1986), Poaceae, Cyperaceae, Velloziaceae, Xyriaceae and Eriocaulaceae are quite common in the region (Giulietti et al., 1987). Species from the genus \textit{Leiothrix} are well represented in these areas and some are even endemic to the mountains of Minas Gerais (Giulietti et al., 1995).

\textit{Study species}

\textit{Leiothrix} individuals are morphologically characterized by their habit of growing in a rosette from which scapes with flower head-type inflorescences appear (Giulietti, 1978). Among the six studied taxa, \textit{L. curvifolia ‘lanuginosa’} (Bong.) Ruhland, \textit{L. curvifolia ‘mucronata’} (Bong.) Ruhland and \textit{L. crassifolia} (Bong.) Ruhland were classified as rhizomatous seed-producing (RS) species, \textit{L. spiralis} (Bong.) Ruhland as a pseudoviviparous rooted (PR) species and \textit{L. vivipara} (Bong.) Ruhland and \textit{L. sinuosa} Giulietti as pseudoviviparous canopy-forming (PCF) species (Fig. 1). RS species usually produce seeds plentifully. Ramets of the PCF species remain attached to the parental rosette suspended by the scapes (Coelho et al., 2006), while the ramets of the PR species take root and may or not remain attached by the scapes to the parental rosette (Coelho et al., 2007).

In \textit{L. curvifolia} and \textit{L. crassifolia} the scapes are shorter than those of pseudoviviparous species (Coelho et al., 2006).

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{fig1.png}
\caption{Schematic illustration of the three groups of reproductive modes. (A) RS group (rhizomatous seed-producing group): \textit{L. curvifolia ‘lanuginosa’}, \textit{L. curvifolia ‘mucronata’} and \textit{L. crassifolia}. (B) PR group (pseudoviviparous rooted group): \textit{L. spiralis}. (C) PCF group (pseudoviviparous canopy-forming group): \textit{L. vivipara}, forming more than one ramet per scape. (D) PCF group: \textit{L. sinuosa}, forming one ramet per scape.}
\end{figure}
Flower head production is intense in those species: on average 15 flower heads are produced per ramet in clones of *L. curvifolia*, and nine flower heads per ramet in clones of *L. crassifolia* (Coelho et al., 2007). The flower heads generally touch the ground when the scapes become curved at the end of the reproductive season (Coelho et al., 2008). Seeds fall in the proximity of the mother rosettes (Coelho et al., 2008). The ramets form compact clones originating from rhizomes (Fig. 1A) (Coelho et al., 2007). The growth of those clones is centripetal, thus the ramets at the centre age earlier than the more peripheral ones. When they die, the clones form rings of densely aggregate ramets (Coelho et al., 2007). Rosettes of *L. spiralis* are morphologically very similar to the rosettes of *L. crassifolia*. In contrast to *L. crassifolia*, in *L. spiralis* the establishment of ramets by way of rhizomes is rare. The formation of a pseudoviviparous propagule in *L. spiralis* is late; it occurs when flower heads are mature and only when they touch the soil (Fig. 1B). However, in *L. vivipara*, propagule formation is early, and occurs just after the flower head formation, and most of them are kept suspended by the scapes (Fig. 1C). The flower heads of the suspended plantlets also proliferate, giving rise to new plantlets. This process may repeat itself several times (Giulietti, 1978). In *L. sinuosa*, pseudoviviparous ramets do not proliferate (Fig. 1D), but, the parental rosette, as is the case in *L. vivipara*, produces many scapes, and the majority of the ramets also remain suspended by them.

*L. curvifolia* taxa that inhabit different microhabitats exhibit a number of reproductive modes. Some species reproduce sexually and give rise to numerous ramets originating from rhizomes, forming compact clones (e.g. *L. curvifolia ‘lanuginosa’*, *L. curvifolia ‘mucronata’* and *L. crassifolia*). Populations of *L. crassifolia* are easily encountered in the Serra do Cipó. *Leiothrix curvifolia ‘lanuginosa’*, apart from being abundant in other locations where it occurs, has a low regional frequency (Giulietti, 1978). One taxon, *L. spiralis*, produces few ramets from rhizomes, but produces pseudoviviparous ramets attached to the parental plant. At the other extreme, some taxa do not produce ramets from rhizomes, but produce numerous pseudoviviparous ramets suspended or rooted, forming more dispersed clones (e.g. *L. vivipara* and *L. sinuosa*).

**Soil sampling**

Soil samples were collected using a borer of 5 cm diameter and 10 cm depth from five populations each of *L. spiralis, L. curvifolia ‘mucronata’* and *L. crassifolia*. For *L. curvifolia ‘lanuginosa’, L. vivipara* and *L. sinuosa*, soil samples were collected from four populations each. 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 (Fig. 2). Analyses of the chemistry, texture and content of organic matter were conducted for each soil sample. The pH was determined potentiometrically in water, CaCl₂ and KCl solution (1 : 2.5). The concentration of hydrogen and aluminium ions was determined by titration with NaOH, and extraction was with Ca(OAc)₂ (0.5 mol L⁻¹, pH 7.0).

The sum of exchangeable bases (SB = Σ K + Ca²⁺ + Mg²⁺ cmol dm⁻³), base saturation [V = Σ bases × 100/CEC (capacity for cationic exchange) cmol dm⁻³], P (mg dm⁻³) and aluminium saturation (m = 100 × Al³⁺/CEC) were determined. The content of organic matter was expressed as a percentage (OM = %C × 1:72). The vegetation cover was also expressed as a percentage (see below, ‘Vegetation cover sampling’). The percentages of coarse sand, thin sand, silt and clay were combined in a single variable denominated ‘texture’ = (silt % + clay %)/ (coarse sand % + thin sand %). This variable expresses the relative water-holding and nutrient capacities. This measurement seems to be more appropriate in sandy or gravel and shallow soils, since the percentage moisture can provide a seasonal measure related to the rainy or dry season.

**Vegetation cover sampling**

Vegetation biomass was collected in the same areas as used for soil sampling. However, a natural fire occurred in the region close to one of the populations of *L. curvifolia ‘mucronata’* and *L. crassifolia* and two populations of *L. vivipara*, and destroyed most of the vegetation. The 72 remaining populations were collected: 15 (5 populations × 3 samples) of *L. spiralis*, 12 (4 populations × 3 samples) of *L. curvifolia ‘mucronata’, L. crassifolia, L. curvifolia ‘lanuginosa’* and *L. sinuosa*, and nine (3 populations × 3 samples) of *L. vivipara*. A quadat of 50 cm² was used. Within each quadat, the percentage vegetation cover was categorized. The categories were recorded by estimating the percentage of the quadat covered by vegetation: low density of vegetation cover – open area <30 %; intermediate density of vegetation cover – sparse area >30 % and <60 %; high density of vegetation cover – densely crowded area >60 %. The vegetation in each area represented cushion and mat plants (mosses), graminoid tussocks, rosette plants and sclerophyllous shrubs belonging mainly to Poaceae, Cyperaceae, Velloziaceae and Xyridaceae. All plant materials were dried for 72 h at 60 °C in a forced draft oven, and then weighed.

**Data analyses**

A discriminant analysis (Kleka, 1980) was performed to test the effect of the microhabitats (soil type and percentage vegetation cover) on the reproductive mode. The classification matrix was jackknifed to correct for the overestimate of classification success caused by using the data set for both generating discriminant functions and classifying cases. The following edaphic and vegetation cover variables were included in the analysis as continuous variables, and were described above (see ‘Soil sampling’ above).

The total amount of nitrogen in soil samples was also measured using Kjeldahls method. The soil nitrogen content, however, was not a good predictor of microhabitat separation. Factorial analyses of variance (ANOVAs) were conducted to compare group means (PCF, PR and RS) for each chemical variable.
RESULTS

The areas of occurrence of the three reproductive modes showed significant differences for the following variables: H + Al, V, OM, biomass and texture (Table 1). The groups of reproductive modes were distinct among soil variables and vegetation cover, as shown by the discriminant analysis (Table 2 and Fig. 3). The $F$-statistic, as well as the $P$-value, was based on Wilks’ lambda, generated by

Table 1. Soil and vegetation cover variables (pH, H + Al, SB, V, P, m, OM, vegetation biomass and texture) measured in populations of the three groups of reproductive modes

<table>
<thead>
<tr>
<th>Variables</th>
<th>PCF</th>
<th>PR</th>
<th>RS</th>
<th>F-values</th>
<th>P-values</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH</td>
<td>4.217 ± 0.06</td>
<td>4.289 ± 0.07</td>
<td>4.251 ± 0.04</td>
<td>0.34</td>
<td>0.711</td>
</tr>
<tr>
<td>H + Al (cmol dm$^{-3}$)</td>
<td>13.378 ± 2.25</td>
<td>9.132 ± 1.39</td>
<td>6.144 ± 0.69</td>
<td>7.38</td>
<td>0.001</td>
</tr>
<tr>
<td>P (mg dm$^{-3}$)</td>
<td>1.795 ± 0.13</td>
<td>1.317 ± 0.07</td>
<td>1.713 ± 0.13</td>
<td>2.17</td>
<td>0.121</td>
</tr>
<tr>
<td>SB (cmol dm$^{-3}$)</td>
<td>0.505 ± 0.07</td>
<td>0.363 ± 0.05</td>
<td>0.352 ± 0.04</td>
<td>1.40</td>
<td>0.253</td>
</tr>
<tr>
<td>m (%)</td>
<td>75.010 ± 2.62</td>
<td>76.794 ± 2.75</td>
<td>74.201 ± 1.76</td>
<td>0.30</td>
<td>0.740</td>
</tr>
<tr>
<td>V (%)</td>
<td>4.421 ± 0.31</td>
<td>4.485 ± 0.54</td>
<td>5.877 ± 0.35</td>
<td>4.88</td>
<td>0.010</td>
</tr>
<tr>
<td>OM (dag kg$^{-1}$)</td>
<td>5.472 ± 0.70</td>
<td>3.667 ± 0.31</td>
<td>3.249 ± 0.21</td>
<td>8.00</td>
<td>0.001</td>
</tr>
<tr>
<td>Biomass (g)</td>
<td>173.196 ± 9.7</td>
<td>29.550 ± 1.58</td>
<td>33.436 ± 1.93</td>
<td>228.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Texture (%)</td>
<td>0.153 ± 0.002</td>
<td>0.083 ± 0.006</td>
<td>0.111 ± 0.008</td>
<td>4.86</td>
<td>0.010</td>
</tr>
</tbody>
</table>

PCF, pseudoviviparous canopy-forming group; PR, pseudoviviparous rooted group; RS, rhizomatous seed-producing group. Means and standard errors as well as $F$-values comparing groups’ means for each variable from factorial ANOVAs are shown.
The jackknife classification matrix results (Table 3) indicated 100 % separation of the PCF group, 56 % separation of the PR group and 72 % of separation of the RS group from the other groups. The total of correctly classified samples was 77 %. The PCF group, that includes *L. vivipara* and *L. sinuosa*, occurs in densely crowded areas, usually with vegetation cover of >60 % and <80 % for *L. vivipara* and of >80 % and <100 % for *L. sinuosa*. The PR group, represented by a single species (*L. spiralis*), occurs preferentially in areas with sparse vegetation of >30 % and <60 %, and in sandy soils and more nutrient-poor soils than the RS group. This latter group (*L. curvifolia ‘mucronata’, L. crassifolia and L. curvifolia ‘lanuginosa’*) also occurs in areas with sparse vegetation of >30 % and <60 %, but in clay and more fertile soils than the PR group. It is common to find, in particular, *L. curvifolia ‘lanuginosa’* growing on mat plants (mosses). In these areas, therefore, the soils have more organic matter than the soils where *L. spiralis* occurs. This is the main factor that separates RS from PR, as shown on the second two axes of the discriminant analysis (Fig. 3).

**DISCUSSION**

Vegetation cover was the primary determinant in the distribution of *Leiothrix* taxa with the varying reproductive modes. Some outcrops in the rupestrian grasslands at the Serra do Cipó are constituted just of exposed sand, without any vegetation cover. However, on contiguous outcrops, a dense vegetation cover can be found, dominated by herbaceous vegetation. Thus, the heterogeneity among close or even contiguous microhabitats can indicate the origin of the different reproductive modes within *Leiothrix*.

The PCF group was separated from the other groups by being found preferentially under densely crowded conditions. The majority of the ramets formed remain supported by the scapes or intertwined with herbaceous leaves (Coelho et al., 2006). Coelho et al. (2005) recorded only one attached plantlet for every 100 supported plantlets, in sites crowded by herbaceous plants. Soils with dense vegetation cover should hold a larger amount of water, and therefore the rosette mothers of *L. vivipara* attached to the soil can invest in the formation of ramets. The herbaceous vegetation promotes intense shading and greater soil moisture. Ramets of pseudoviviparous plants are photosynthetically active (Lee and Harmer, 1980; Pierce et al., 2003); therefore, each suspended ramet is a photosynthetic
unit of a dispersed ‘canopy’ where the light incidence is more intense. To remain suspended by the scapes reaching the top of the herbaceous cover, the ramets can acquire necessary photosynthates and translocate them to the rosettes attached to the soil through their scapes. The development of a canopy-forming strategy in this species was possible because: (a) the formation of pseudoviviparous ramets is early, occurring just after flower head formation; (b) the flower heads of the suspended ramets also proliferate, giving rise to new ramets; and (c) it is difficult for the ramets to touch the ground in sites where there is crowding of herbaceous plants.

The PR reproductive mode occurs preferentially in microhabitats with sparse vegetation. Few pseudoviviparous ramets of *L. spiralis* grow amongst herbaceous vegetation, which would impede contact of those ramets with the soil. The PR reproductive mode seems to be an efficient strategy for reproduction and ramet spreading, enhancing their chances of survival (Coelho et al., 2006). This guerrilla-type expansion strategy, as occurs in *L. spiralis*, is associated with fast habitat occupancy, spatial exploration (Harper, 1985; Fahrig et al., 1994) and low resource supply (de Kroon and Hutchings, 1995; Ye et al., 2006). A higher spatial spread favoured by the guerilla growth form can be advantageous, if it allows escape of *L. spiralis* ramets from uncrowded conditions. Therefore, it is likely that vegetation cover exerts selection pressure on the clonal growth form of this plant. As in *L. spiralis*, the ramets are formed only after the flower head touches the ground; few pseudoviviparous ramets of this species grow amongst herbaceous vegetation, which would be impede contact of those plantlets with the soil (Coelho et al., 2006).

The RS group, comprising *L. curvifolia* ‘lanuginosa’, *L. curvifolia* ‘micronata’ and *L. crassifolia*, also prevailed in soils with sparse herbaceous vegetation. These species form compact clones (phalanx-type) originating from rhizomes and they produce numerous seedlings originating from seeds (Coelho et al., 2008). Although the rupestrian grassland soils are inherently nutrient poor, rhizomes are usually thought to store buds and resources in order to be able to regenerate in more favourable conditions (Grace 1993; Dong and de Kroon, 1994). Moreover, among ramets of the clone, a continuous flow of mineral nutrients stored in the rhizomes and photosynthates acquired from the ramets can occur. This can ensure the survival and the growth of the ramets and clones in nutrient-poor areas (Humphrey and Pike, 1998). Sackville Hamilton et al. (1987) suggested that sexual reproduction may be more important for clonal plants with a phalanx growth form than for those with a guerrilla growth form, because phalanx plants depend more on seeds for colonization of available microhabitats than guerrilla plants do, which would be in accordance with the present findings, that the seedling recruitment is more important than the clonal recruitment in the RS species studied. Mainly because the rupestrian grassland soils are inherently nutrient poor, specific microhabitats might have acted as strong selective pressure toward the rhizomatous seed-producing strategy.

Several studies show that the microenvironmental heterogeneity can generate differentiation in the growth form and reproductive modes, and may generate adaptive radiation (Harper et al., 1961; Monasterio and Sarmiento, 1991; Bengtsson et al., 1994; Rauscher, 2002; Verboom et al., 2004; Ellis et al., 2006; Friar et al., 2006). Verboom et al. (2004) showed an association between life history strategy and habitat (native substrate) for eight *Ehrharta*, a group of grasses that radiated in arid environments of the Cape region of South Africa. Ellis et al. (2006) were studying evolutionary radiation of ‘stone plants’ in *Argyroderma*, and found four groups of strategies for the plants occupying different edaphic microenvironments. Ecologists have considered that at smaller spatial scales, related species that co-occur in local communities usually exhibit spatial or temporal differentiation in microhabitat (Ackerly et al., 2006). It is at this local scale that the ecological differentiation influences the co-existence of closely related species (Ackerly et al., 2006). Habitat divergence plays a crucial role in sympatric or parapatric speciation, because the evolution of reproductive barriers must somehow take place in the presence of gene flow (Welch and Rieseberg, 2002; Rajakaruna, 2004). Since ecological speciation involves niche shifting in an environmental mosaic (Levin, 2005), microhabitat specialization may thus be an important mechanism maintaining the reproductive modes within *Leiothrix*. According to Levin (2005), ecological speciation is a more likely venue for major changes within genera. The large number of endemic species within *Leiothrix* in Serra do Cipó therefore supports the ecological speciation hypothesis. This view is in accord with the proposition of Levin (2003, 2004, 2005). Although speciation by polyploidy is considered more common in plants than in animals, it accounts for only 2–4 % of plant speciation events (Schluter, 2001). Thus, even in plants, most speciation events can be due to divergent natural selection influenced by abiotic or biotic environmental forces (Schluter, 2001; Levin, 2003).

The present results suggest that reproductive mode diversification within *Leiothrix* occupying different microenvironments probably results from response to fine-scale habitat variation. Moreover, the results suggest a possible role for microhabitat specialization in reproductive mode diversification of *Leiothrix* and perhaps in its broader radiation in Serra do Cipó. Clonal propagules from rosettes of *Leiothrix* have extremely local dispersal capabilities, and even seed-producing taxa do not possess mechanisms especially adapted to long-distance dispersal, which is essential to facilitate local adaptation in fine-scale habitat mosaics.

In conclusion, the findings of the present study corroborate the hypothesis that microenvironmental heterogeneity has acted on the reproductive mode variation of *Leiothrix*, and that habitat mosaics of the rupestrian grasslands have played an important role in the broader radiation of *Leiothrix* in Serra do Cipó. In addition, it is proposed that ecological speciation, driven by divergent natural selection on reproductive traits and resulting from features of the environment, is an important process in adaptive radiation in this genus, since none of the *Leiothrix* taxa studied seems able to grow in all available habitats. Such an inability can cause diversification of reproductive strategies
in space and may enhance the possibilities for sympatric speciation (Tuomisto, 2006). Finally, this study provides the first speculations about the processes underlying the phenomenal radiation of Leiothrix in the rupestral grasslands in Brazil, and provides support for the hypothesis of Levin (2003) that changes in the ecological attributes of populations, especially involving habitat and resource utilization, are an important component of speciation in flowering plant lineages.

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LITERATURE CITED


