Pollination of two species of *Vellozia* (Velloziaceae) from high-altitude quartzitic grasslands, Brazil

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RESUMO – (Polinização de duas espécies de *Vellozia* (Velloziaceae) de campos quartzíticos de altitude, Brasil). Foram pesquisados os polinizadores e o sistema reprodutivo de duas espécies de *Vellozia* (Velloziaceae) de campos rupestres quartzíticos do sudeste do Brasil. *Vellozia leptopetala* é arborescente e cresce exclusivamente sobre afloramentos rochosos, *V. epidendroides* é de porte herbáceo e espalha-se sobre solo pedregoso. Ambas têm flores hermafroditas e solitárias, e floradas curtas em massa. Avaliou-se o nível de auto-compatibilidade e a necessidade de polinizadores, em 50 plantas de cada espécie e 20-60 flores por tratamento: polinização manual cruzada e autopolinização, polinização espontânea, agamospermia e controle. O comportamento dos visitantes florais nas flores e nas plantas foi registrado. As espécies são auto-incompatíveis, mas produzem poucas sementes autogâmicas. A razão pólen-óvulo sugere xenogamia facultativa em ambas. Foram visitadas principalmente por abelhas, das quais as mais importantes polinizadoras foram duas cortadeiras (*Megachile* spp.). *Vellozia leptopetala* também foi polinizada por uma espécie de beija-flor territorial. A produção de sementes em frutos de polinização cruzada sugere que limitação por pólen é a causa principal da baixa produção natural de sementes. Isto foi atribuído ao efeito combinado de cinco mecanismos: autopolinização prévia à antese, elevada geitonogamia resultante de arranjo floral, número reduzido de visitas por flor pelo mesmo motivo, pilhagem de pólen por diversas espécies de insetos e, em *V. leptopetala*, deposição de pólen heteroespecífico em conseqüência da promiscuidade dos beija-flores.

Palavras-chave: limitação polínica, geitonogamia, campos rupestres, auto-incompatibilidade, Serra do Cipó

ABSTRACT – (Pollination of two species of *Vellozia* (Velloziaceae) from high-altitude quartzitic grasslands, Brazil). The pollinators and breeding system of two species of *Vellozia* (Velloziaceae) from high-altitude quartzitic grasslands in SE Brazil were studied. *Vellozia leptopetala* is shrubby and grows solely on rocky outcrops, *V. epidendroides* is herbaceous and grows on stony soils. Both bear solitary, hermaphrodite flowers, and have massive, short-lasting annual blooms. We evaluated the level of self-compatibility and need for pollinators of 50 plants of each species and 20-60 flowers per treatment: hand self- and cross-pollination, spontaneous pollination, agamospermy and control. The behavior of floral visitors on flowers and within plants was recorded. Both species are mostly self-incompatible, but produce a small number of seeds by self-fertilization. The pollen-ovule ratio suggests facultative xenogamy. They were visited primarily by bees, of which the most important pollinators were two leaf-cutting bees (*Megachile* spp.). *Vellozia leptopetala* was also pollinated by a territorial hummingbird. Low natural seed production compared to cross-pollination seed numbers suggests that pollen limitation is the main cause of low seed set. This was attributed to the combined effect of five mechanisms: selfing prior to anthesis, enhanced geitonogamy as a result of large floral displays, low number of visits per flower for the same reason, pollen theft by many insect species, and, in *V. leptopetala*, delivery of mixed pollen loads on the stigma as a consequence of hummingbird promiscuity.

Key words: pollen limitation, geitonogamy, rocky grasslands, self-incompatibility, Serra do Cipó

Introduction

Lack of suitable pollination, together with resource limitation, have been two important factors traditionally held responsible for incomplete fruit and seed set, particularly self-progeny (Queller 1985; Haig & Westoby 1988; Guitián & Navarro 1996; Collevatti *et al*. 1997; Lindell 1998; Niesenbaum 1999). The causes and consequences of pollen limitation in particular have been the object of much attention in recent years (Ashman *et al*. 2004).

Reduced seed set by pollen limitation is often the result of combined quantitative and qualitative mechanisms. Quantitative pollen limitation has been related to lack of suitable pollinators, in association with a temporary lack of visits because of climate, habitat alterations or heterogeneity (Schiller *et al*. 2000; Moody-Weiss & Heywood 2001; Montgomery *et al*.

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2003), competition with other floral resources (but see Feldman *et al*. 2004), or initial colonization of a new area (Larson *et al*. 2002). Qualitative pollen limitation is closely related to the plant breeding system and derives from visits that do not necessarily bring the correct kind of pollen to the stigma. It has been claimed to result from either increased self-pollination (de Jong *et al*. 1993, and references therein; Shibayama & Kadono 2003) or heterospecific pollen transfer (Fishman & Wyatt 1999; Brown & Mitchell 2001; Yang *et al*. 2005), and floral display is pointed out as a key factor affecting these processes. A poor floral display will be overlooked by visitors, resulting in small quantities of pollen deposited and removed. On the other hand, a large floral display attracts more pollinators to the plant but these tend to visit more flowers on each plant, increasing the rate of self-pollen transfer within the plant, albeit less than proportionally (Robertson 1992; Robertson & MacNair 1995; Schiller *et al*. 2000; Ohashi & Yahara 2002). Although exceptions have been reported (Ohara & Higashi 1994), a long sequence of visits to flowers in a plant is usually detrimental for seed set (e.g. Iwasa *et al*. 1995), both in self-incompatible species, resulting in little or no seed production, and self-compatible species, which usually manifest some degree of inbreeding depression. Evaluating the causes and effects of enhanced self-pollination is particularly important in self-incompatible, massive blooming species, as is the case of several Velloziaceae.

Velloziaceae is a small family of approximately 250 species of fibrous shrubby plants (Mello-Silva 2005). Its members grow mainly in edaphically dry localities of South America, Africa and Madagascar. Individuals are typical elements of tropical inselbergs (rock hilltops), and bear resistance characteristics such as quiescence (Owoseye & Sanford 1972), drought-enduring leaves (sclerophylly), and adventitious roots with multi-layered *velamen* which allow them to quickly absorb any available water from rain or mist (Porembski & Barthlott 1995). They are also adapted to fire (Alves 1994; Ibisch *et al*. 1995). The family has many representatives in the 'campo rupestre' vegetation (high-altitude rocky grasslands) of the Espinhaço Range, SE Brazil (Giulietti & Pirani 1988). The region has a very high level of endemism, probably associated with altitudinal isolation (Alves & Kolbek 1994).

In contrast with the great taxonomic interest in the family (Mello-Silva 2005), there are very few works focusing on the ecology or pollination biology of Velloziaceae from the Espinhaço Range (Sazima & Sazima 1990; Landau *et al*. 1998). Our objectives were to study the breeding system and pollinator behaviour of two sympatric species of *Vellozia*, *V. leptopetala* Goeth. & Henr. and *V. epidendroides* Mart. ex Schult. & Schult., which differ in microhabitat preference and genetic diversity (Franceschinelli *et al*. 2006).

Material and methods

Study site – The study took place in 'campo rupestre' vegetation (19º17' S, 43º35' W, *ca*. 1,200 m a.s.l.), at the southern portion of the Espinhaço Range, a quartzitic formation with mean and maximum altitudes of 1,000 m and 2,000 m respectively, and N-S orientation. The region is characterized by a Köppen type Cwb climate (mesothermic), with a wet summer season and mean annual rainfall of 1,500 mm concentrated during November-March (Nimer 1989). The vegetation is composed of savanna-like communities and gallery forests at lower altitudes, and campo rupestre vegetation beginning at approximately 1,000 m (Giulietti *et al*. 1987).

Biological material – The flowers of both species are bisexual, regular and solitary, and have a petaloid perianth; the ovary is inferior, with three locules and ovules on stalked placentas; the style is slender and ends in a dry, capitate stigma. The 18 anthers are bright yellow, pollen is abundant and shed in tetrads (Smith & Ayensu 1976). Anthesis is diurnal, and flowers remain receptive for two to three days (Sazima & Sazima 1990; Oliveira *et al*. 1991). Fruits are dry, hard capsules. Seeds are tiny (1.1-1.5 mm diam) and spheroid, and show no particular mechanism for dispersal, although it has been suggested they are wind-dispersed (Ibisch *et al*. 2001). Populations of both species occur throughout Serra do Cipó, and *V. epidendroides* extends 200 km further north.

Vellozia leptopetala individuals grow exclusively on rocky outcrops in campos rupestres. Plants are woody in appearance, 0.5-1.5 m high. Populations are characterized by annual synchronous blooms that last less than a month, some weeks after the first spring rains. Flowers are large (3.4-4.0 cm diam), white, with six narrow and patent tepals that turn reflexive and with lilac shades after the first day (Fig. 1A). According to Sazima and Sazima (1990), these modifications, together with the tube-like arrangement of the purple filaments, denote evolved adaptations for hummingbird pollination in this otherwise melittophilous genus.

Vellozia epidendroides individuals are short with a slender pseudostem (30-40 cm high), and grow in well-defined patches over extensive areas in open stony grasslands (Fig. 1B). Each ramet bears a solitary large (3.5-4.2 cm diam) white flower, with six broad tepals suberect at anthesis. The flowering period is less concentrated than that of *V. leptopetala*, and different patches of the species bloom from late summer (March) throughout May.

Methods – Individual flowers were manipulated to test the level of self-compatibility as well as the need for pollinating agents, on 50 plants of each species. Four pollination treatments were performed: 1) hand cross-pollination, by emasculation, followed by pollinating each flower with pollen from two plants distant at least 100 m from the recipient (n = 40 flowers on 30 plants), 2)

hand self-pollination, by pollinating a flower with its own pollen (n = 40 on 20 plants), 3) agamospermy, by emasculation (n = 20 flowers on 20 plants), and 4) spontaneous self-pollination, in which buds were bagged and left to pollinate spontaneously (n = 40 for *V. epidendroides* and 60 for *V. leptopetala*, on 20 plants). Each treatment flower was bagged with fine-mesh (ca. 0.3 mm width) nylon net until the fruit was fully developed. In addition, 40 unmanipulated flowers from 30 plants were bagged after the stigma ceased to be receptive and used as control, open-pollinated flowers. Twenty-five pre-anthesis flowers of each species were bagged to measure daily nectar volume and sugar concentration. To calculate pollen-ovule (P/O) ratios, pollen grains from one anther and ovules from one locule of three different flowers were counted with the aid of gridded slides.
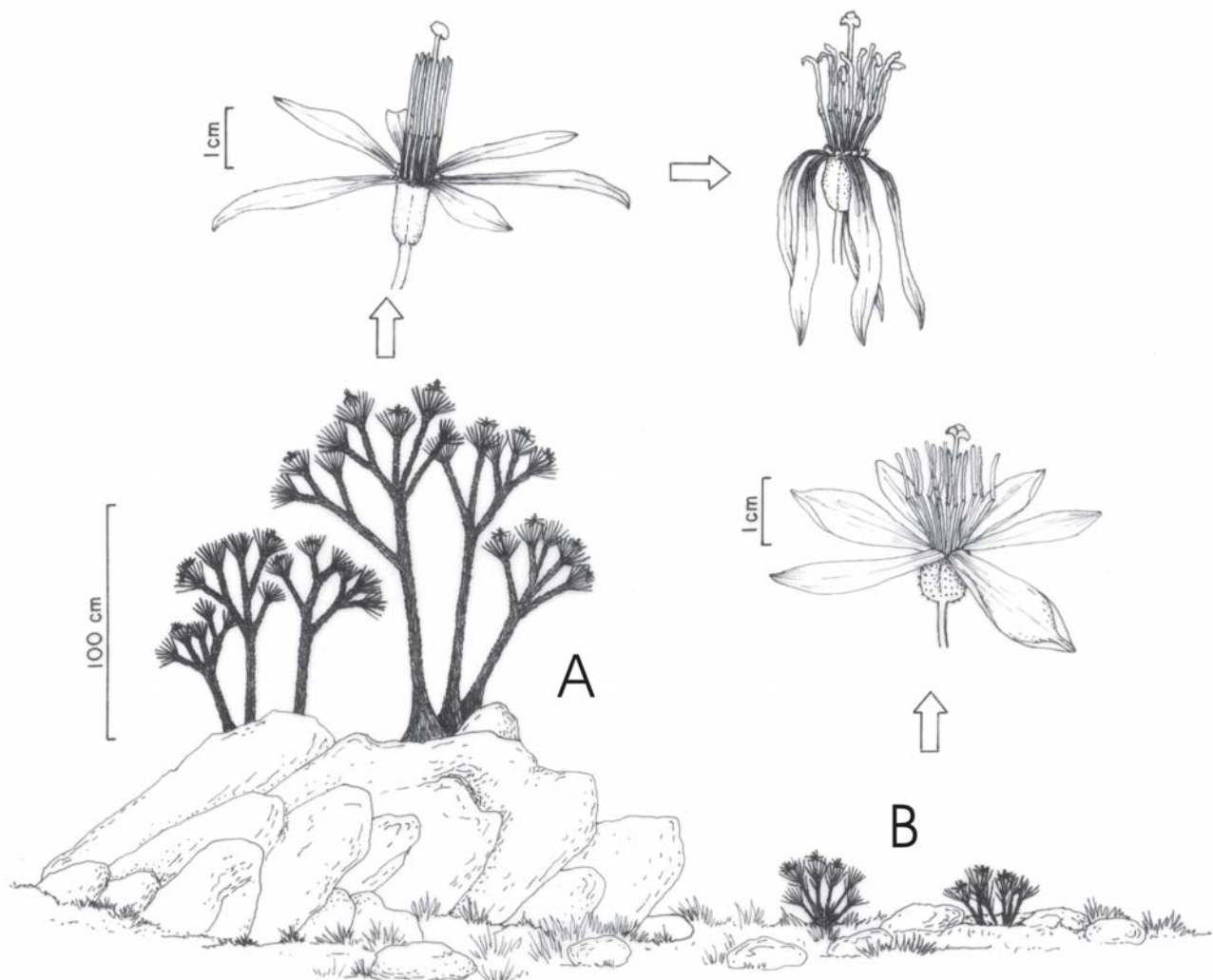

Figure 1. Habit and flower morphology. A) *Vellozia leptopetala,* growing on rocky outcrops (detail shows changes from first- to second-day flower), B) *V. epidendroides*, growing on pebbly ground, Serra do Cipó, MG.

After maturation, we collected the fruits and recorded the number of seed per fruit. Few marked flowers were lost or damaged throughout fruit development. To calculate mean seed number, however, we excluded seedless fruits. Welch's approximate t statistic was used to check for difference in seed set among treatments (Zar 1996). Two indices associated with the mating system were calculated, following Lloyd and Schoen (1992): the self-compatibility index (SCI), which is the ratio of hand self-pollination to hand cross-pollination seed set, and the self-fertility index (SFI), which is the ratio of spontaneous to hand cross-pollination seed set. Voucher specimens were deposited in the BHCB Herbarium (Botany Department, Federal University of Minas Gerais, Brazil).

Floral visitor activity was recorded during 240 hours of field observations, usually from 0600 to 1800 h (early morning until sunset, approximately) during the flowering season of each species. The approach, resource gathering and movements regarding contact with stigma were recorded for all visitors. Hummingbirds were photographed and identified by comparison with collection specimens. Insects were captured with an entomological net, mounted and identified, and deposited in the first author's insect collection.

Results

Reproductive biology and floral features – The large patches of *V. epidendroides* bearing hundreds of white flowers with bright yellow anthers are very conspicuous in the rupestrian landscape. Although large individuals of *V. leptopetala* can reach 200 flowers, the floral display is less striking because tepals are slender, they bend down and acquire darkish hues in second-day flowers. Tepals of both species wither and darken after three to four days, and remain attached throughout fruit development or they are readily removed by florivores. Anthesis in both species starts in the early morning, and flowers are odorless. Anther dehiscence is longitudinal, synchronous, and may occur from one hour before anthesis to 2-3 hours after tepals are fully displayed. Deposition of self-pollen on the stigma before tepals spread is common. Nectar in *V. leptopetala* is produced in the hypanthium, in small volumes (5.22 ± 1.45 µl/24h, n=25) and low sugar concentration (11.62 ± 3.31 %, n=25), but no measurable quantities of nectar were extracted from the other species. In both species,

the number of pollen grains (about 777,600) divided by the number of ovules (900-1300) per flower corresponds to facultative xenogamy on Cruden's (1977) classification.

The results of the pollination treatments are shown in Table 1. Seedless capsules (fruits do not abscise) were abundant in both species except for control and cross-pollinated flowers. *Vellozia epidendroides* produced only 23% of fruits with few selfed-seeds when manually pollinated. This contrasted with the small number of seedless fruits (7.5%) and the mean number of seeds per fruit (194.4 ± 148.0, n=37) derived from cross-pollination. No seeds resulted from either agamospermy or spontaneous pollination. Cross-pollination seed set was significantly larger than control (df = 40, p<0.0001) and self-pollination (df = 43, p<0.0001), and no significant difference was found between control and self-pollination seed set (df = 14, p = 0.34). *Vellozia leptopetala*, on the other hand, produced more fruits with selfed-seeds, both from spontaneously pollinated (40%) and hand-pollinated flowers (28%). As with *V. epidendroides*, no seeds resulted from agamospermy. There was a significant difference in mean seed set only between cross-pollinated fruits (484.5 ± 318.0, n = 35) and all other treatments. There was no statistical difference between the number of control and selfed-seeds (df = 15, p = 0.15). Although autogamous fruits produced a small number of seeds, self-incompatibility and the need for pollinators was confirmed for both species by means of the indices SCI and SFI, whose values were lower than an established cut-off point of 20%.

Floral visitors – Both species were visited by a diversity of insects, of which only bees were effective pollinators. During peak hours (1000-1300 h) flowers received 9.8 ± 9.4 visits per hour. Medium and large bees predominated over social and small bees with respect to species number but not to relative abundance (Table 2). All bee visitors collected exclusively pollen.

The foraging strategy of bees depended on their size. In general, large bees (Megachilidae and most Apidae) landed either on the stigma, anthers, or even tepals, and usually touched both stigma and anthers with the hind legs and ventral part of abdomen and thorax in their search for pollen. They foraged from early morning until approximately 1600 h. Small bees (Halictini, Ceratinini, and Trigonini) landed directly on the anthers and seldom touched the stigma while collecting pollen or when flying away. They

Table 1.   Seeds produced by different pollination treatments in *Vellozia epidendroides* and *V. leptopetala* (Velloziaceae), Serra do Cipó, MG. n/N = number of fruits with seeds / number of flowers treated. The ratios of self to cross (SCI) and of spontaneous to cross-pollinated fruits (SFI) were calculated based on the mean seed number of fruits with seeds only.

Treatments	*V. epidendroides*			*V. leptopetala*		
	mean ± SD	(min-max)	n/N	mean ± SD	(min-max)	n/N
Agamospermy	0		0/20	0		0/20
Self-pollination						
manual	31.2 ± 28.0	(3-92)	9/40	42.3 ± 40.4	(11-119)	11/40
spontaneous	0		0/40	37.9 ± 42.6	(7-200)	24/60
Cross-pollination	194.4 ± 148.0	(18-622)	37/40	484.5 ± 318.0	(11-1250)	35/40
Control	35.9 ± 33.1	(3-122)	34/40	59.6 ± 45.8	(6-130)	28/40
SCI	0.16			0.09		
SFI	0			0.08		

concentrated their visits between 0700 and 1000 h, and were rarely seen after 1400 h. The two species of *Dialictus*, as well as small social Apidae such as *Ceratina* sp., *Trigona spinipes*, *Geotrigona subterranea*, *Paratrigona lineata* and *P. subnuda*, were classified as thieves of both *Vellozia*, because their size allows them to reach and scrape the anthers without touching the stigma (which they did very rarely). All other bees were considered legitimate pollinators.

Six bees were common to both species (Table 2). Of these, *Apis mellifera*, *Megachile* (*Chrysosarus*) sp., and *Paroxystoglossa* sp. were the most frequent. *Apis mellifera* individuals remained for several minutes foraging on a single flower, and agonistic encounters with other species were common. They remained for most time in a single plant, compared to other visitors, which restricted their visits to less than a minute per flower and foraged on fewer flowers per plant. *Vellozia epidendroides* was visited by 16 bee species, with different importance as pollinators (Table 2). *Megachile* (*Chrysosarus*) and *A. mellifera* were the most common. Augochlorini were frequent in the morning, whereas most Apidae were more common in the afternoon. Visits by large and medium bees such as *Diadasiana riparia*, *Melipona quinquefasciata*, *Xylocopa* spp., *Tetrapedia* sp. 1, and *Centris* sp. were uncommon, but they always touched the stigma while foraging. *Vellozia leptopetala* attracted fewer bee species, three of which were frequent pollinators, three infrequent, and three occasional (Table 2). The most common bees were *Paroxystoglossa* sp. and *Dialictus* sp. 1. Most bees initiated their visits around 0700 h and reduced their visits in the afternoon, although *Dialictus*, *Megachile* (*Chrysosarus*), *Trigona*

spinipes, *Ceratina* and *A. mellifera* were still active until approximately 1700 h. This species was intensively visited by *Augastes scutatus* (Temminck), a territorial hummingbird, which foraged from dawn till dusk. Hummingbirds visited 50-100% of the flowers in each plant, including second-day flowers, which were less visited by bees. Although they concentrated their visits on *V. leptopetala*, hummingbirds visited other nearby flowering species such as *Vellozia declinans*, *Cuphea* sp. and *Vochysia* sp. during the same foraging bout.

Discussion

Seed set in harsh environments may be affected by reduced resources, and the rupestrian flora is known to be subjected to different levels of climatic and edaphic stress (Alves & Kolbek 1994; Fernandes *et al.* 1996; Scatena & Moraes 1996; Jacobi *et al.* 2000). *Vellozia* species, however, are among the plants best adapted to these environments (Gaff 1987; Alves & Kolbek 1994; Porembski & Barthlott 2000), through drought-resistance structures, mechanisms which allow for quick uptake of water and mist, and by synchronizing flower production with rainfall. It is therefore likely that seed production in *V. epidendroides* and *V. leptopetala* is primarily pollen-limited due to the combination of several mechanisms that promote wrong pollen deposition and an inadequate number of legitimate visits, as discussed below.

The few works available on the breeding system of *Vellozia* had already pointed out that several species are self-incompatible (Oliveira *et al.* 1991; M. Sazima unpubl. data). These studies, however, did not contemplate a quantitative survey of seeds. Here we confirmed self-sterility in both species with basis on

Table 2. Bee visitors of *Vellozia leptopetala* and *V. epidendroides*, Serra do Cipó, MG. Pf = frequent pollinator, Pi = infrequent pollinator, Oc = thief, but occasional pollinator, Th = thief.

Family/Tribe	Species	*V. leptopetala*	*V. epidendroides*
HALICTIDAE			
Augochlorini	*Augochloropsis cleopatra* (Schrottky)		Oc
	Augochloropsis sp.	Oc	
	Paroxystoglossa sp.	Oc	Oc
	Pseudaugochlora graminea (Fabricius)	Oc	
Halictini	*Dialictus* sp. 1	Th	
	Dialictus sp. 2	Th	
MEGACHILIDAE			
Megachilini	*Megachile (Chrysosarus)* sp.	Pf	Pf
	Megachile (Pseudocentron) sp.	Pf	Pf
APIDAE			
Apini	*Apis mellifera* L.	Pf	Pf
Ceratinini	*Ceratina (Ceratinula)* sp.	Th	
Centridini	*Centris (Hemisiella)* sp.	Pi	
	Centris sp.		Pi
Emphorini	*Diadasina riparia* (Ducke)		Pi
Meliponini	*Melipona quinquefasciata* Lepeletier		Pi
Tetrapediini	*Tetrapedia* sp. 1		Pi
	Tetrapedia sp. 2	Pi	
Trigonini	*Geotrigona subterranea* (Friese)		Th
	Paratrigona lineata (Lepeletier)		Th
	Paratrigona subnuda Moure		Th
	Trigona spinipes (Fabricius)	Th	Th
Xylocopini	*Xylocopa truxali* Hurd & Moure		Pi
	Xylocopa (Neoxylocopa) sp.	Pi	Pi
	Xylocopa (Schonnherria) sp.		Pi
Total species		13	16

the number of seeds per fruit, and provide evidence for facultative xenogamy based on their P/O ratios. Dispersal of pollen grains in tetrads and pollinator efficiency probably contribute to a lower P/O ratio than that expected with basis only on the degree of self-incompatibility (Cruden & Miller-Ward 1981). Seed set occurred in a few fruits produced by spontaneous (only in *V. leptopetala*) and manual self-pollination. A similar pattern for *V. squamata*, a "cerrado" (Brazilian savanna) species was proposed by Oliveira *et al.* (1991) to be a post-fertilization rejection mechanism, included broadly in the late-acting self-incompatibility category. Overall, ovarian and other late-acting self-incompatibility systems are still under investigation (Oliveira *et al*. 1991), and this validates efforts to examine the causes and effects of self-pollination.

Different mechanisms of self-pollen transfer were identified in both *Vellozia*. One is anther dehiscence prior to flower opening. At this time the style is in touch with the anthers, and self-pollen is deposited on the stigma. Not all flowers, however, opened their anthers

before anthesis, so a proportionally more important mechanism promoting self-pollination is geitonogamy. *Vellozia leptopetala*, in particular, has a massive floral display, which leads bees and hummingbirds to visit many flowers in each plant. A long sequence of visits within a plant results in a high percentage of geitonogamous pollination (Robertson 1992; Robertson & MacNair 1995; Ohashi & Yahara 2002), detrimental in both species given their high level of self-incompatibility. Finally, given that there is no specific mechanism for seed dispersal and this is probably limited to a few meters from the mother plant, it is also possible that a considerable percentage of outgoing pollen is transferred among genetically related plants in the neighborhood, and contributes to inbreeding depression resulting in low seed set.

Wrong-pollen delivery by heterospecific pollen transfer is equally detrimental for seed set, but probably less frequent, and occurs mainly in *V. leptopetala*. The promiscuous behavior of hummingbirds, which visit more than one plant species while foraging, could result

in heterospecific pollen loads and stigma clogging. No foreign pollen was present in the bees captured, so hummingbirds appear to be the only pollinators involved in significant improper pollen transfer. Sazima and Sazima (1990) reported lack of bees visiting *V. leptopetala* in a nearby area of comparable altitude, and attributed this to trends towards ornithophily represented by changes in floral morphology and color, together with dilute nectar. In agreement with their conclusions, and although we recorded several bee species in *V. leptopetala*, visits were mostly to first-day flowers, and individuals collected exclusively pollen. The changes in color and tepal display suffered by second-day flowers, and possibly aided by pollen depletion, makes this species less attractive to bees and comparatively more visited by hummingbirds.

In spite of a high frequency of visits, it is possible that the system is pollinator-limited because of two reasons. First, large floral displays are known to attract more visitors but the number of visits per individual flower may be proportionally reduced (Robertson 1992; Iwasa *et al*. 1995; Robertson & MacNair 1995; Larson & Barrett 2000; Ohashi & Yahara 2002). Second, in both species the amount of pollen removed without effective pollen delivery was substantial, because visits from legitimate pollinators, represented by large and medium bees, were rare with few exceptions. In addition, theft was common, performed by several small bees and also by *A. mellifera*. This bee, even if a legitimate pollinator, is an expensive one, because it removes large amounts of pollen of which only a small portion is deposited on stigmas. Because it is a social species, the proportion of visits was high compared to solitary bees.

Although the plants studied share several life history characters and most of the mechanisms promoting pollen limitation, the intensity of some of these was different, and were used to help explain differences in genetic variability between V. *leptopetala* and V. *epidendroides* found in a research performed on the same populations of this study (Franceschinelli *et al.* 2006). Overall, *V. leptopetala* showed high inbreeding within isolated patches and lower genetic diversity than *V. epidendroides*. The former, which grows exclusively on outcrops and is therefore more subjected to genetic isolation and geitonogamy, has a territorial hummingbird as one of the main pollinators. This territorial behavior would restrict pollen spread to nearby plants, adding to the negative effects of limited seed dispersal, as discussed above. *Vellozia epidendroides*, which relies only on

bees for pollination, could retain genetic diversity by means of a larger, less synchronized and less isolated floral display. Finally, the clonal growth of both species may explain the maintenance of high levels of self-incompatibility, which is known to decline in association with abiotic factors that reduce the efficacy of pollinators, such as altitude, isolation, and xeric or exposed environments (Levri 1998).

Acknowledgments

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