

Germination Patterns and Seed Longevity of Monocotyledons from the Brazilian Campos Rupestres

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ABSTRACT

The Brazilian campos rupestres vegetation is associated with the Espinhaço Mountain chain, a region recently declared a Biosphere Reserve by UNESCO, in recognition of its high diversity and large numbers of endemic species. The campos rupestres vegetation typically occupies exposed rocky areas, sandy plains, and swamps, at above 900 meters, and is generally composed of a mix of herbaceous plants and sparse shrubs and subshrubs. The proposal of this study was to present a revision of the biometry, germination behavior, and longevity of the seeds of four families of monocotyledons occurring in the campos rupestres. The family Bromeliaceae is widely distributed in Brazil, while Eriocaulaceae, Xyridaceae, and Velloziaceae are quite abundant in the campos rupestres of the Espinhaço Mountains. The seeds of all the species analyzed were small, with average lengths of 0.6-2.6 mm and average dry weights of 0.0019-0.49 mg. The seeds of the Bromeliaceae are generally aphotoblastic, while those of Eriocaulaceae, Xyridaceae, and Velloziaceae are positive photoblastic. In general, the seeds demonstrate high germination rates over a wide range of temperatures (most will germinate between 15-35°C). The analysis of seed longevity in the soil indicated that, except for the Bromeliaceae, all of the species examined maintained their viability in the soil for more than a year and thus had the potential to form persistent soil seed banks. The persistence of these seeds in the soil is related to their small size and to light requirements for germination – characteristics that contribute to successful recruitment in open environments like the campos rupestres, with high solar radiation levels and wide temperature fluctuations.

Keywords: Bromeliaceae, Eriocaulaceae, photoblastism, rocky fields, seed germination, seed size, seed bank, temperature, Velloziaceae, Xyridaceae

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INTRODUCTION

Studies of patterns that can lead to a better understanding of the population dynamics of the vegetation in a given region become imperative given the current stage of degradation of the ecosystems. The implementation of restoration and management strategies for ecosystems depends on information concerning the requirements for seed germination, seed dormancy patterns, seed size, as well as their viability and longevity (Jensen 2004). Seed germination is a process that depends on the specific environmental conditions that influence seedling establishment (Baskin and Baskin 1988), and promote the selection for diversified germination characteristics among the species (Vázquez-Yanes and Orozco-Segovia 1993). Germination reflects the habitats, life strategies, phylogenetic relationships, and the geographical distribution of the parent species (Schultz and Rave 1999). Similar life strategies and life cycles are generally expected among congeneric species, and differences observed among them may reflect specific adaptations to the habitats that they occupy (Specht and Keller 1997; Assche *et al.* 2002).

Brazil has one of the world's richest floras, with approximately 19% of all known plant species, including 14% of the described monocotyledon species of which 45% are endemic. Among the monocotyledon families with the greatest numbers of species in Brazil are the Bromeliaceae, Eriocaulaceae, Velloziaceae, and Xyridaceae (Giulietti *et al.* 2005). Approximately 30% of the world's Bromeliaceae, more than 45% of the Xyridaceae and Eriocaulaceae, and 85% of the world's Velloziaceae occur in Brazil. The degrees of endemism for these same families are approximately 65% for Bromeliaceae, 70% for Xyridaceae, and more than 95% for Eriocaulaceae and Velloziaceae (Giulietti *et al.* 2005). The family Bromeliaceae is widely distributed in Brazil (Reitz 1983; Giulietti *et al.* 2005), while Eriocaulaceae, Xyridaceae, and Velloziaceae are particularly abundant in the campos rupestres vegetation of the Espinhaço Mountain chain, where ca. 90% of their species are endemic (Giulietti *et al.* 2005).

The proposal of the present work was to present a short review of the biometry, germination behavior, and longevity of seeds from various species of four monocotyledon

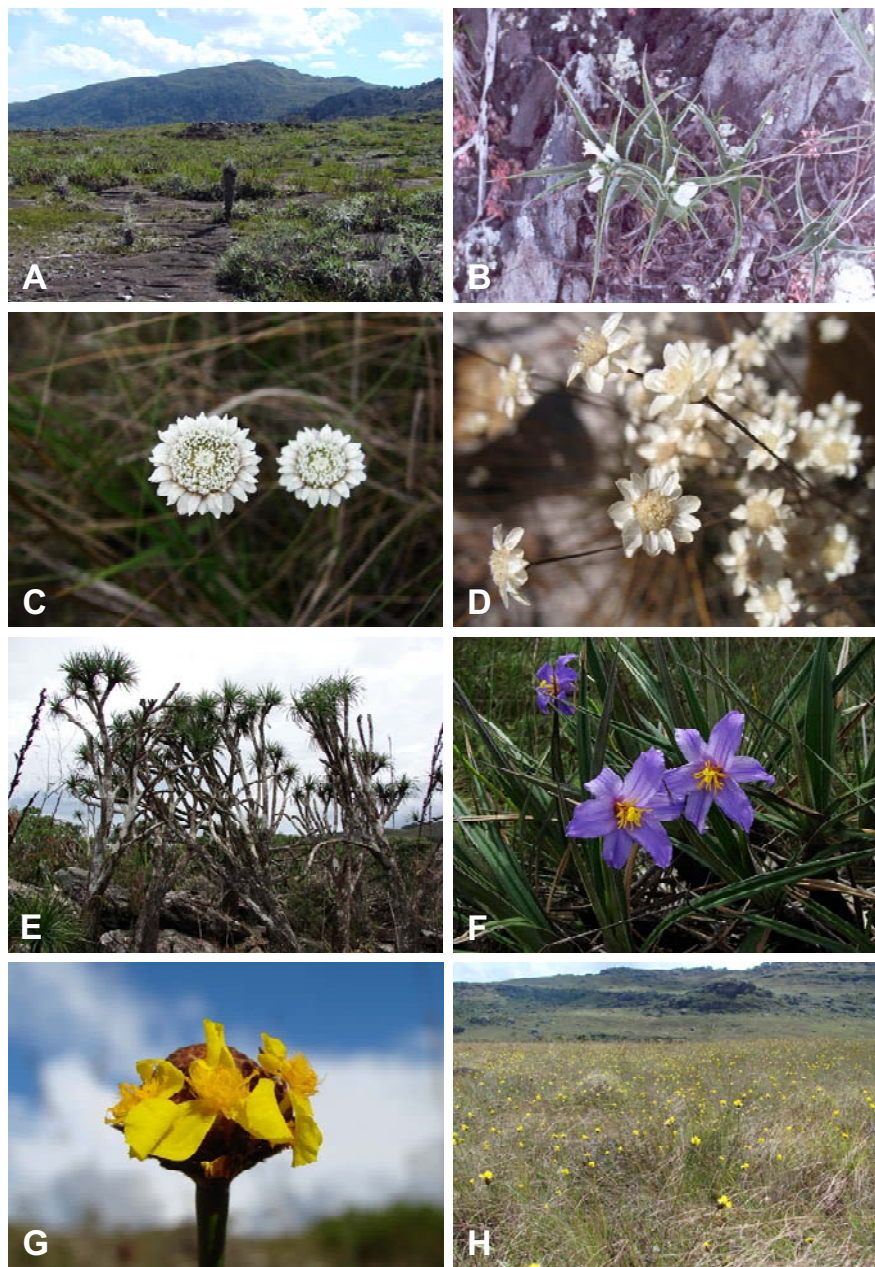


Fig. 1 Campos rupestres vegetation. Campos rupestres (A); *Cryptanthus shawakeanus* (B); *Paepalanthus* sp. (C); *Syngonanthus* sp. (D); *Vellozia gigantea* (E); *V. variabilis* (F); *Xyris plathystachya* (G); *Xyris* field (H). Photos courtesy of PL Viana (A, G, H), AR Marques (B), U Oliveira (C, F), FMG Santos (D), LA Soares (E).

families common to the Brazilian campos rupestres vegetation. These parameters are considered essential to our understanding of the processes of seedling establishment and of the succession and regeneration of the native vegetation (Vázquez-Yanes and Orozco-Segovia 1993), and will contribute to the management and conservation of this important ecosystem.

CHARACTERIZATION OF THE CAMPOS RUPESTRES

The campos rupestres vegetation has generated considerable research interest due to its unique biotic and abiotic characteristics (Giulietti *et al.* 1987). This vegetation type is associated with the Espinhaço Mountain chain that extends for 1000 km (north to south) between northern Bahia State and central Minas Gerais State, Brazil (Giulietti *et al.* 1987). The region is characterized by quartzitic mountains with altitude varying between 1000-1400 m, reaching 1800 m in certain areas (Menezes and Giulietti 1986). The climate is considered mesothermic, with mild summers and a rainy period during the summer, when temperature vary from 17 to 20°C. The annual precipitation is nearly 1500 mm; there

is a dry period during the winter, which lasts 6-7 months, and a moist period, that lasts 5-6 months (Coelho *et al.* 2006).

Campos rupestres vegetation typically occupies exposed rocky areas, sandy plains, and swamps, at altitudes generally greater than 900 m (Menezes and Giulietti 2000), and it is characterized principally by an herbaceous plant layer associated with sparse shrubs and subshrubs (Fig. 1A). Campos rupestres plants are usually sclerophyllous, perennially green, with imbricate or rosette leaves; with convergent morphology observed in numerous families (Menezes and Giulietti 1986). It is considered one of the richest and most diverse vegetation types in the world due to its high degree of endemism (Giulietti *et al.* 1987; Giulietti and Pirani 1988) and high degree of adaptive radiation, especially prevalent in some families that have their centers of dispersal in this region. Campos rupestres vegetation is often discontinuous, and species usually occur as disjointed populations. Each population has a degree of speciation that is highly dependent on the specific environment that it occupies, resulting in the formation of autochthonous floras with extremely restricted areas (Giulietti and Pirani 1988).

The Espinhaço Mountain chain was recently declared a

Biosphere Reserve by UNESCO in recognition of its high diversity and its large numbers of endemic species. Many of these species are included in the IUCN Red List of species threatened of extinction due to their limited areas of occurrence and the presence of strong anthropogenic forces altering their habitats such as mining, fire, and the predatory collection of a number of species of economic/ornamental value (Menezes and Giulietti 2000).

CHARACTERIZATION OF THE PLANT FAMILIES

Bromeliaceae is a predominantly neotropical family (Dahlgren 1985) with approximately 50 genera and at least 2219 species (Giulietti *et al.* 2005). The species of this family are herbaceous epiphytes or terrestrial plants, with leaves arranged in rosettes and densely imbricate on a short stem that terminates in a spike or a paniculate inflorescence, usually with brightly colored bracts (**Fig. 1B**) (Tomlinson 1969). In Minas Gerais State alone, 18 species of Bromeliaceae are included on the Red List of threatened plants (Mendonça and Lins 2000).

The Eriocaulaceae are perennial (rarely annual) herbaceous plants growing in terrestrial, swamp, or aquatic environments. The family is characterized by a generally rosette growth habit from which the scapes emerge, forming a capitulate inflorescence (**Fig. 1C, 1D**). The family has approximately 1200 species distributed among 11 genera (Giulietti *et al.* 2005) with pantropical distributions, although the species are concentrated in the neotropical region (Giulietti and Hensold 1991).

The family Xyridaceae comprises 5 genera and 300 species distributed throughout the tropical and subtropical regions (Wanderley 1992; Giulietti *et al.* 2005). These plants are usually perennial and acaulescent, the leaves are spirally or distichously arranged below long floral scapes, and the flowers are arranged in spikes (**Fig. 1G, 1H**) (Wanderley 1992). In Brazilian campos rupestres, are usually found in flat, sandy areas (Machado and Sajo 1996), preferentially in wet sites (Tomlinson 1969).

Some species of Eriocaulaceae and Xyridaceae are popularly known and commercially collected as dry-flowers ("sempre-vivas"), for the scapes and inflorescences of these species retain a life-like appearance even after harvesting and drying. These plants are much used for ornamental purposes and have significant economic value, especially the species of Eriocaulaceae (Teixeira 1987; Giulietti *et al.* 1988). The scapes and inflorescences are collected indiscriminately before the seeds can be dispersed, however, thus

diminishing the recruitment of new individuals and placing many species at risk of extinction (Giulietti *et al.* 1988, 1996; Menezes and Giulietti 2000). The IUCN Red List includes 31 species of Eriocaulaceae (of which 16 are probably extinct) and nine species of Xyridaceae.

The family Velloziaceae has showy flowers with white, yellow or purple tepals (**Fig. 1E, 1F**). This family is essentially tropical and comprises nine genera and approximately 250 perennial herbaceous or shrub species (Ayensu 1973; Mello-Silva 1991; Giulietti *et al.* 2005). Minas Gerais State has the largest number of species and these demonstrate a high degree of endemism, with a number of species considered to be threatened of extinction (Mello-Silva 1991, 1995). The IUCN Red List includes 23 species from this family, of which seven are probably extinct (Mendonça and Lins 2000).

SEED SIZE

The processes of germination and growth are directly related to seed size (Harper *et al.* 1970; Leishman *et al.* 2000), and seed size can, in turn, be associated with the environments in which the plants occur (Westoby *et al.* 1992). Large seeds are associated with shaded habitats (Venable and Brown 1988; Leishman *et al.* 2000), while small seeds are associated with open (Venable and Brown 1988; Leishman and Westoby 1994; Seiwa and Kikuzawa 1996) or disturbed environments (Fenner 1995) and generally need light to germinate (Thompson and Grime 1983; Bewley and Black 1994; Rosa and Ferreira 2001). There is evidence to support the view that the size and the mass of a seed are inversely proportional to its longevity in the soil (Thompson 2000; Moles *et al.* 2003). This situation may be related to the fact that small seeds are more easily buried and tend to suffer less damage from predation (Thompson 2000).

The study done by Norbert and Annette (2004) with 152 species, which correlated seed mass and seed accumulation index, revealed that species whose seeds have masses <~0.14 mg generally demonstrate a strong tendency to accumulate in the soil, while seeds with masses >2.7 mg are almost completely absent from the soil seed bank.

The species examined in this study were all herbaceous perennial plants, with the exception of *V. alata* and *V. leptopetala* (subshrubs that grow to 1.5 to 2.0 m), and *V. gigantea* (a shrub species than can reach up to 5 m in height). The data available on Brazilian campos rupestres species indicates that seeds of the families Eriocaulaceae and Xyridaceae are very small, varying from 0.36 to 1.13 mm in

Table 1 Average length, width, and dry weight of monocotyledon seeds (average \pm SE) from the *campos rupestres* of Brazil.

Families and Species	Length (mm)	Wide (mm)	Dry mass (mg)	Reference
Eriocaulaceae				
<i>Paepalanthus chlorocephalus</i>	1.13 \pm 0.11	0.82 \pm 0.08	**	Kraus <i>et al.</i> 1996
<i>P. gemiculatus</i>	0.68 \pm 0.05	0.40 \pm 0.04	**	Kraus <i>et al.</i> 1996
<i>P. incanus</i>	0.82 \pm 0.06	0.51 \pm 0.05	**	Kraus <i>et al.</i> 1996
<i>P. senaeamus</i>	0.90 \pm 0.06	0.60 \pm 0.06	**	Kraus <i>et al.</i> 1996
<i>Syngonanthus elegantulus</i>	0.36 \pm 0.04	0.21 \pm 0.02	0.013 \pm 0.00010	Oliveira and Garcia 2005
<i>S. elegans</i>	0.37 \pm 0.04	0.22 \pm 0.02	0.015 \pm 0.00025	Oliveira and Garcia 2005
<i>S. venustus</i>	0.50 \pm 0.04	0.24 \pm 0.03	0.025 \pm 0.00013	Oliveira and Garcia 2005
<i>S. nitens</i>	0.89 \pm 0.09	0.32 \pm 0.06	0.033 \pm 0.0007	Schmidt <i>et al.</i> 2007
Velloziaceae				
<i>Vellozia epidendroides</i>	1.15 \pm 0.01	*	**	Garcia <i>et al.</i> 2007
<i>V. gigantea</i>	1.45 \pm 0.05	*	0.47 \pm 0.02	Garcia and Diniz 2003
<i>V. glandulifera</i>	2.60 \pm 0.05	*	0.49 \pm 0.01	Garcia and Diniz 2003
<i>V. leptopetala</i>	1.31 \pm 0.06	*	**	Garcia <i>et al.</i> 2007
<i>V. variabilis</i>	1.01 \pm 0.01	*	0.21 \pm 0.01	Garcia and Diniz 2003
Xyridaceae				
<i>Xyris cipoensis</i>	1.06 \pm 0.22	0.37 \pm 0.04	0.0100 \pm 0.0002	Abreu and Garcia 2005
<i>X. longiscapa</i>	0.56 \pm 0.08	0.19 \pm 0.02	0.0019 \pm 0.0002	Abreu and Garcia 2005
<i>X. platystachia</i>	0.92 \pm 0.10	0.33 \pm 0.05	0.0075 \pm 0.0008	Abreu and Garcia 2005
<i>X. trachyphylla</i>	0.66 \pm 0.08	0.22 \pm 0.03	0.0031 \pm 0.0002	Abreu and Garcia 2005

* Due to the irregular form of the seeds, their length was considered as being the greatest distance between their extremities.

** Data not available.

length and 0.21 to 0.82 mm in width (**Table 1**). The maximum dry masses recorded for these seeds were 0.033 mg for Eriocaulaceae and 0.0075 mg for Xyridaceae. Although species of the family Velloziaceae demonstrated larger seeds than the previous two families described, their dry masses were still below 0.5 mg (**Table 1**), and as such can be classified as small seeds. There is essentially no published data available concerning seed size for species of Bromeliaceae growing in the campos rupestres. Our field observations, and the data from two species analyzed (*Dyckia minarum* 0.56 mg and *Dyckia* sp 0.72 mg, unpublished data), indicate that the species of this family tend to have small seeds. This confirms the published literature, as a majority of the Monocotyledonae are herbaceous species and have average seed masses of about 1.5 mg (Moles *et al.* 2005).

LIGHT AND TEMPERATURE

Comparisons of the germination requirements of related species may demonstrate how the germination processes have adapted to local environmental conditions (Assche *et al.* 2002). Temperature is one of the principal environmental factors controlling germination (Baskin and Baskin 1988; Bewley and Black 1994; Benech-Arnold and Sánchez 1995), and the best temperature range for germination is generally associated with the temperatures that the plants are exposed to during their growth phase (Baskin and Baskin 1988, 1992; Angosto and Matilla 1993; Villalobos and Peláez 2001). Temperature influences germination rate and the germination percentages as it affects the rate of water absorption and modifies the rates of the chemical reactions that

mobilize and metabolize the stored seed reserves (Bewley and Black 1994). Seeds germinate within a defined temperature range that is characteristic of each species, and this range can determine the geographical distribution of those plants (Thompson 1973; Labouriau 1983; Probert 1992).

A majority of the Bromeliads analyzed had quiescent seeds. Of the 12 species examined, nine were aphotoblastic over wide temperature ranges (**Table 2**). The seeds of these species were not inhibited by darkness, and germination can thus occur in the cracks in a rock or in fissures in a tree trunk, or in the soil (even if the seeds were covered by stones, grasses or leaf litter) (Marques 2002). *Cryptanthus schwackeanus* and *Dyckia saxatilis* demonstrated positive photoblastic behavior, while *Tillandsia aeris-incola* was negative photoblastic at temperatures above 20°C (**Table 2**). According to Marques (2002), the response of *T. aeris-incola* may be related to the fact that this species is only found in montane forests where the environment tends to be heavily shaded.

The seeds of Eriocaulaceae, Xyridaceae, and Velloziaceae can be considered positive photoblastic as they demonstrate restricted photoblastism or greater germination percentage in the presence of light over a wide range of temperatures (**Table 2**). Only the seeds of *Vellozia gigantea*, *V. variabilis* (Garcia and Diniz 2003), and *V. epidendroides* (Garcia *et al.* 2007) demonstrated high germinability in the dark at high temperatures, behaving as aphotoblastic at these temperatures (**Table 2**).

The campos rupestres families analyzed demonstrated certain peculiarities: the species of Velloziaceae demonstrated high germinability and wide temperature ranges for germination; the Xyridaceae demonstrated restricted posi-

Table 2 Germination temperature range, photoblastic behavior at different temperatures, maximum germination percentage, and habitat types of monocotyledon species from the Brazilian *campos rupestres* vegetation. Restricted positive photoblastic (RPP), Positive photoblastic (PP), Negative photoblastic (NP), and aphotoblastic (AP); Xeric (Xe), Mesic (Me), and Wet (We). All the germination tests were conducted in laboratory.

Species	Temperature (°C)	Photoblastism	Germination (maximum %)	Habitat	Reference
Bromeliaceae					
<i>Aechmea nudicaulis</i>	15-35	AP	90	Xe and Me	Marques 2002
<i>Neoregelia bahiana</i>	15-35	AP	90	Xe	Marques 2002
<i>Cryptanthus schwackeanus</i>	20-35	RPP	90	Xe	Marques 2002
<i>Dyckia saxatilis</i>	15-35	PP (15-30°C)/AP (35°C)	70	Xe	Marques 2002
<i>Vriesea bituminosa</i>	15-35	AP	100	Xe and Me	Marques 2002
<i>V. citrina</i>	15-35	AP	90	Xe	Marques 2002
<i>V. crassa</i>	15-35	AP	100	Xe	Marques 2002
<i>V. friburgensis</i>	15-35	AP	100	Xe	Marques 2002
<i>V. gutata</i>	15-35	AP	100	Xe and Me	Marques 2002
<i>Tillandsia aeris-incola</i>	15-35	AP (15-20)/NP (25-35)	100	Me	Marques 2002
<i>T. gardneri</i>	15-35	AP	100	Xe and Me	Marques 2002
<i>T. stricta</i>	15-35	AP	100	Xe and Me	Marques 2002
Eriocaulaceae					
<i>Paepalanthus chlorocephalus</i>	30 *	PP	78		Kraus <i>et al.</i> 1996
<i>P. geniculatus</i>	30 *	PP	84		Kraus <i>et al.</i> 1996
<i>P. incanus</i>	30 *	PP	98		Kraus <i>et al.</i> 1996
<i>P. senaeamus</i>	30 *	PP	88		Kraus <i>et al.</i> 1996
<i>Syngonanthus elegantulus</i>	15-35	RPP	36.5	Me	Oliveira and Garcia 2005
<i>S. elegans</i>	15-35	PP	75	Xe	Oliveira and Garcia 2005
<i>S. nitens</i>	22/30 **	PP	92	Me and We	Schmidt <i>et al.</i> 2007
<i>S. niveus</i>	26 *	PP	61		Kraus <i>et al.</i> 1996
<i>S. venustus</i>	15-35	PP	67.5	We	Oliveira and Garcia 2005
Velloziaceae					
<i>V. epidendroides</i>	20-40	PP (20 - 30)/AP (35 e 40)	93	Xe	Garcia <i>et al.</i> 2007
<i>V. gigantea</i>	20-40	PP (20 - 30)/AP (35 e 40)	96	Xe	Garcia and Diniz 2003
<i>V. glandulifera</i>	15-40	PP	95	Xe	Garcia and Diniz 2003
<i>V. leptopetala</i>	15-40	PP	100	Xe	Garcia <i>et al.</i> 2007
<i>V. variabilis</i>	20-40	PP (20-35)/AP (40)	95	Xe	Garcia and Diniz 2003
Xyridaceae					
<i>Xyris cipoensis</i>	20-30	RPP	81	We	Abreu and Garcia 2005
<i>X. longiscapa</i>	15-30	RPP	87	Xe	Abreu and Garcia 2005
<i>X. platystachia</i>	15-30	RPP	98	We	Abreu and Garcia 2005
<i>X. trachyphylla</i>	15-30	RPP	96	Xe	Abreu and Garcia 2005

* Germination tests were only performed at the temperatures cited.

** Temperature alternated with the 16 hr photoperiod.

tive photoblastism, high germinability, although within more restricted temperature ranges (especially *X. cipoensis*, which had the most restricted distribution area among all the species analyzed in this study); the Bromeliaceae and the Eriocaulaceae had essentially the same temperature ranges for germination and the lowest germinability, even though they differed in relation to their light requirements and have very distinct geographical distributions.

The light requirement for the germination of small seeds represents an impediment to the initiation of the germination process while they are still buried under the soil. These seedlings would have more difficulty in emerging from greater soil depths due to their limited growth reserves (Pearson *et al.* 2003) that would become exhausted before reaching the soil surface and initiating photosynthesis (Harper 1977; Bewley and Black 1994). Another relevant factor related to the necessity of light (and the importance of quickly initiating the photosynthetic processes) is the fact that germinating seedlings *in vitro* of species of Eriocaulaceae and Xyridaceae generally begins to develop their aerial portions at the 4th day, while adventitious roots form slightly later, usually at the 20th day after germination (Scatena *et al.* 1993; Kraus *et al.* 1996; Scatena *et al.* 1996). The photodormancy of species of Eriocaulaceae, Xyridaceae, and Velloziaceae is associated with the small size of their seeds and indicates a selection for open environments exposed to the high illumination and wide temperature fluctuations common in the campos rupestres environment.

The germination of positive photoblastic species is controlled by phyB (a form of phytochrome responsible for the detection of changes in the red/far-red, and which controls the processes of germination by low fluence responses/LFR). However, high temperatures induce the formation of phyA (responsible for germination by very low fluence responses/VLFR) and can promote seed germination even in the dark (Takaki 2001). This phenomenon may help to explain the high germinability observed in the three species of *Vellozia* under experimental conditions of darkness and high temperatures. However, temperatures above 30°C have not been reported in shaded micro-habitats (e.g. rock clefts) or below the soil surface in areas of campos rupestres. As such, we can infer that seeds do not commonly encounter temperatures favorable to germination in the dark (35 and 40°C) in the campos rupestres.

SEED LONGEVITY

The soil seed bank includes all viable seeds on the soil surface or mixed within that soil (Leck *et al.* 1989). This bank is an efficient mechanism for vegetation recomposition (Baker 1989; Simpson *et al.* 1989) and is of fundamental importance for recruitment after any environmental disturbances (McGee and Feller 1993). Seeds banks are classified as transient when the seeds survive for less than one year, short-term persistent when the seeds remain viable for periods >1 year and <5 years, and long-term persistent when seed viability extends over even longer periods of time (Thompson 1993).

The seeds that compose the soil seed bank are dispersed in a state of innate (primary) dormancy (Baker 1989; Pons 1991; Bewley and Black 1994), such as photodormancy and/or a specific temperature regime to germinate (Vásquez-Yanes and Orozco-Segovia 1993). Their persistence in the soil is also related to their small size (Thompson and Grime 1983; Pons 1991).

Studies examining the physiology of germination among seeds artificially stored in soil have been important in evaluating the longevity and behavior of seeds under natural conditions without the interference of predators (Vásquez-Yanes and Orozco-Segovia 1993), although the results of these experiments are sometimes open to diverse interpretations (Bakker *et al.* 1990). Studies of the longevity of the seeds of three species of *Syngonanthus* incorporated into an artificial seed bank are presented in **Table 3**. The seeds were placed in fine-mesh nylon bags and then buried

Table 3 Germination in laboratory of recently collected seeds (RC) of *Syngonanthus* (Eriocaulaceae) and of seeds stored for 12 and 24 months in soil from the Serra do Cipó Range, Minas Gerais State, Brazil.

Species	Germinability (%)		
	RC	12 months	24 months
<i>Syngonanthus elegantulus</i>	35.5	24.5	14
<i>S. elegans</i>	75	34.5	7.5
<i>S. venustus</i>	67	10	12.5

at about 5 cm deep in the area of occurrence of *Syngonanthus*, and germination tests were carried in laboratory under 12-hr photoperiod at optimal temperature for each species, 25°C (*S. elegantulus*) and 30°C (*S. elegans* and *S. venustus*). After 24 months, *S. elegans* and *S. venustus* had lost 90 and 80% of their germination ability, respectively, while 40% of the seeds of *S. elegantulus* remained viable (**Table 3**). In spite of significant reductions in the viability of the seeds of these three species over time, the results indicated that they do form a persistent seed bank. Similar studies with seeds of Velloziaceae (Diniz 2002) and Xyridaceae (Abreu 2004) in artificial soil seed banks have demonstrated that these plants can also form persistent seed banks, as some of the seeds remain viable for 18 and 24 months, respectively. As mentioned earlier, the seeds of *Syngonanthus*, as well as those of Velloziaceae and Xyridaceae, are small and positive photoblastic – characteristics that favor longevity in the soil. Within the family Bromeliaceae, only the seeds of *C. schwackeanus* and *D. saxatilis* demonstrate any potential for persistence in the seed bank due to photodormancy. The seeds of the other species, being quiescent, require only the presence of water, and they can germinate immediately after dispersal and do not depend on the illumination regime.

The maintenance of genetic diversity in seed banks is a source of long-term stability for plants populations (Epling *et al.* 1960). The formation of persistent soil seed banks is extremely important for campos rupestres species, especially for those threatened of extinction or considered to be in a critical situation. By remaining dormant, but viable, for indeterminate periods of time these seeds can assure the recruitment of new individuals through germination when favorable environmental conditions appear (Vásquez-Yanes and Orozco-Segovia 1993).

CONCLUSIONS

The Bromeliaceae family demonstrates a wide geographical distribution, and differed from the other families analyzed here in terms of having aphotoblastic seeds – a situation that prevents a majority of the bromeliad species from forming soil seed banks. The families Eriocaulaceae, Velloziaceae, and Xyridaceae, which are typical monocotyledons and which have many endemic species in the campos rupestres of the Espinhaço Mountain Range (Brazil), demonstrated convergence in all of the parameters analyzed here: small seeds that are positive photoblastic over a wide temperature range, and the potential for forming persistent soil seed banks. The persistence of the seeds of these latter three families in the soil seed bank is related to their small size and to their light requirements for germination – characteristics that contribute to recruitment success in open environments in the campos rupestres commonly exposed to high levels of solar illumination and wide temperature fluctuations. However, although these characteristics are indicative of adaptation to this exposed environment, they should not be interpreted as the only sources of the high degrees of endemism observed in these three families in the campos rupestres biome.

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REFERENCES

- Abreu MEP, Garcia QS (2005) Efeito da luz e da temperatura na germinação de sementes de quatro espécies de *Xyris* L. (Xyridaceae) ocorrentes na Serra do Cipó, MG, Brasil. *Acta Botanica Brasílica* **19**, 149-154
- Abreu MEP (2004) Germinação e formação de banco de sementes de espécies de *Xyris* (Xyridaceae) da Serra do Cipó. MSc Thesis, Universidade Federal de Minas Gerais, Belo Horizonte, Brasil, 41 pp
- Assche JV, Diane Van Nerum DV, Darius P (2002) The comparative germination ecology of nine *Rumex* species. *Plant Ecology* **159**, 131-142
- Ayensu ES (1973) Biological and morphological aspects of the Velloziaceae. *Biotropica* **5**, 135-149
- Angosto T, Matilla AJ (1993) Variations in seeds of three endemic leguminous species at different altitudes. *Physiologia Plantarum* **87**, 329-334
- Baskin JM, Baskin CC (1988) Germination ecophysiology herbaceous plant species in a temperature region. *American Journal of Botany* **75**, 286-305
- Baskin JM, Baskin CC (1992) Role of temperature and light in the germination ecology of buried seeds of weedy species of disturbed forests I. *Lobelia inflata*. *Canadian Journal of Botany* **70**, 589-592
- Baker H G (1989) Some aspects of the natural history of seed banks. In: Leck MA, Parker VT, Simpson RL (Eds) *Ecology of Soil Seed Banks*, Academic Press, London, pp 9-21
- Bakker JP, Poshlod P, Strykstra RJ, Bekker RM, Thompson K (1996) Seed banks and seed dispersal: Important topics in restoration ecology. *Acta Botanica Neerlandica* **45**, 461-490
- Bewley JD, Black M (1994) *Seeds: Physiology of Development and Germination* (2nd Edn), Plenum Press, New York, 445 pp
- Benech-Arnold R, Sánchez RA (1995) Modeling weed seed germination. In: Kigel J, Galili G (Eds) *Seed Development and Germination*, Academic Press, New York, pp 545-566
- Coelho FF, Capelo C, Neves ACO, Martins RP, Figueira JEC (2006) Seasonal timing of pseudoviviparous reproduction of *Leiotrix* (Eriocaulaceae) rupestrian species in South-eastern Brazil. *Annals of Botany* **98**, 1189-1195
- Diniz ISS (2002) Comportamento germinativo e potencial para formação de banco de sementes em espécies de Velloziaceae da Serra do Cipó (MG). MSc Thesis, Universidade Federal de Minas Gerais, Belo Horizonte, Brasil, 47 pp
- Dahlgren RMT, Clifford HT, Yeo PF (1985) *The Families of the Monocotyledons: Structure, Evolution and Taxonomy*, Springer-Verlag, Berlin, 520 pp
- Epling C, Lewis H, Ball F (1960) The breeding group and seed storage: a study in populations dynamics. *Evolution* **14**, 238-255
- Fenner M (1995) Ecology of seed banks. In: Kigel J, Galili G (Eds) *Seed Development and Germination*, Academic Press, New York, pp 507-543
- Garcia QS, Diniz ISS (2003) Comportamento germinativo de três espécies de *Vellozia* da Serra do Cipó (MG). *Acta Botanica Brasílica* **17**, 487-494
- Garcia QS, Jacobi CM, Ribeiro BA (2007) Resposta germinativa de duas espécies de *Vellozia* (Velloziaceae) dos campos rupestres de Minas Gerais, Brasil. *Acta Botanica Brasílica* **21**, 451-456
- Giulietti AM, Pirani JR (1988) Patterns of geographic distribution of some plant species from Espinhaço Range, Minas Gerais and Bahia Brasil In: Vanzoloni PE, Heyer HR (Eds) *Proceedings of Workshop on Neotropical Distribution Patterns*, Academia Brasileira de Ciências, Rio de Janeiro, pp 39-69
- Giulietti AM, Hensold NC (1991) Synonymization of the genera *Comanthera* and *Carpotepala* with *Syngonanthus* (Eriocaulaceae). *Annals of the Missouri Botanical Garden* **78**, 273-295
- Giulietti AM, Wanderley MGL, Longhi-Wagnre HM, Pirani JR, Parra JR (1996) Estudos em "sempre-vivas": taxonomia com ênfase nas espécies de Minas Gerais, Brasil. *Acta Botanica Brasílica* **10**, 329-384
- Giulietti N, Giulietti AM, Pirani JR, Menezes NL (1988) Estudos de sempre-vivas: importância econômica do extrativismo em Minas Gerais, Brasil. *Acta Botanica Brasílica* **1**, 179-194
- Giulietti AM, Menezes NL, Pirani JR, Meguro M, Wanderley MGL (1987) Flora da Serra do Cipó, Minas Gerais: caracterização e lista de espécies. *Boletim de Botânica da Universidade de São Paulo* **96**, 1-152
- Giulietti AM, Harley RM, Queiróz LP, Wanderley MGL, van den Berg C (2005) Biodiversity and conservation of plants in Brazil. *Conservation Biology* **19**, 632-639
- Harper JL, Lovell PH, Moore KG (1970) The shapes and size of seeds. *Annual Review of Ecology and Systematics* **1**, 327-356
- Harper JL (1977) *Populations Biology of Plants*, Academic Press, New York, 892 pp
- Jensen K (2004) Dormancy patterns, germination ecology, and seed bank types of twenty temperate fen grassland species. *Wetlands* **24**, 152-166
- Kraus JE, Scatena VL, Lewinger ME, Sá Trench KU (1996) Morfologia externa e interna de quatro espécies de *Paepalanthus* Kunth (Eriocaulaceae) em desenvolvimento pós-seminal. *Boletim de Botânica da Universidade de São Paulo* **15**, 45-53
- Labouriau LG (1983) *A Germinação das Sementes*, Secretaria Geral da Organização dos Estados Americanos. Washington, DC, 179 pp
- Leishman MR, Westoby M (1994) The role of large seed size in shaded conditions: experimental evidence. *Functional Ecology* **8**, 205-214
- Leishman MR; Wright IJ, Moles AT, Westoby M (2000) The evolutionary ecology of seed size. In: Fenner M (Ed) *The Ecology of Regeneration in Plant Communities*, CAB International Wallingford, UK, pp 31-72
- Leck MA, Parker VT, Simpson RL (1989) *Ecology of Soil Seed Banks*, Academic Press, London, 462 pp
- Marques AR (2002) Ecofisiologia e contribuições para a conservação das bromélias da Serra da Piedade. PhD Thesis, Universidade Federal de Minas Gerais, Belo Horizonte, 120 pp
- Mcgee A, Feller MC (1993) Seed banks of forested and disturbed soils in southwestern British Columbia. *Canadian Journal of Botany* **71**, 1574-1583
- Machado SR, Sajo MG (1996) Ocorrência de camada protetora no complexo estomático de folhas de *Xyris hymenachne* Mart. (Xyridaceae). *Naturalia* **21**, 63-68
- Mello-Silva R (1991) The infra-familial taxonomic circumscription of the Velloziaceae: A historical and critical analysis. *Taxon* **40**, 45-51
- Mello-Silva R (1995) Aspectos taxonômicos, biogeográficos, morfológicos e biológicos das Velloziaceae de Grão-Mogol, Minas Gerais, Brasil. *Boletim de Botânica da Universidade de São Paulo* **14**, 49-79
- Mendonça MP, Lins LV (2000) *Lista vermelha das espécies ameaçadas de extinção da flora de Minas Gerais*, Fundação Biodiversitas & Fundação Zoológica de Belo Horizonte, Brasil, 157 pp
- Menezes NZ, Giulietti AM (1986) Campos rupestres: Flora da Serra do Cipó. *Ciência Hoje* **5**, 38-44
- Menezes NZ, Giulietti AM (2000) Campos rupestres. In: Mendonça MP, Lins LV (Eds) *Lista Vermelha das Espécies Ameaçadas de Extinção da Flora de Minas Gerais*, Fundação Biodiversitas & Fundação Zoológica de Belo Horizonte, Brasil, pp 65-73
- Moles AT, Warton DI, Westoby M (2003) Seed size and survival in the soil in arid Australia. *Australian Ecology* **28**, 575-585
- Moles AT, Ackery DD, Webb CO, Tweddle JC, Dickie, Westoby M (2005) A brief history of seed size. *Science* **307**, 576-580
- Oliveira PG, Garcia QS (2005) Efeito da luz e da temperatura na germinação de sementes de *Syngonanthus elegantulus* Ruhland, *S. elegans* (Bong.) Ruhland e *S. venustus* Silveira (Eriocaulaceae). *Acta Botanica Brasílica* **19**, 639-645
- Norbert H, Annette O (2004) Assessing soil seed bank persistence in flood-meadows: The search for reliable traits. *Journal of Vegetation Science* **15**, 93-100
- Pearson TRH, Burslem DFRP, Mullins CE, Daling JW (2003) Functional significance of photoblastic germination in neotropical pioneer trees: a seed's eye view. *Functional Ecology* **17**, 394-402
- Pons TL (1991) Induction of dark dormancy in seeds: its importance for the seed bank in the soil. *Functional Ecology* **5**, 669-675
- Probert RJ (1992) The role of temperature in germination ecophysiology In: Fenner M (Ed) *The Ecology of Regeneration in Plant Communities*, CAB International Wallingford, UK, pp 285-325
- Reitz R (1983) Bromeliáceas e a Malária-Bromélia Endêmica In: Reitz R (Ed) *Flora Ilustrada Catarinense*, Itajaí, Santa Catarina, pp 1-58
- Rosa SGT, Ferreira AG (2001) Germinação de sementes de plantas medicinais lenhosas. *Acta Botanica Brasílica* **15**, 147-288
- Scatena VL, Menezes NL (1993) Embryology and seedling development in *Syngonanthus rufipes* Silveira (Eriocaulaceae). *Beitraege Zur Biologie der Pflanzen* **67**, 333-343
- Scatena VL, Lemos FJP, Lima AAA (1996) Morfologia do desenvolvimento pós-seminal de *Syngonanthus elegans* e *S. niveus* (Eriocaulaceae). *Acta Botanica Brasílica* **10**, 85-91
- Seiwa K, Kikuzawa K (1996) Importance of seed size for the establishment of seedlings of five deciduous broad-leaved tree species. *Vegetation* **123**, 51-64
- Schmidt IB, Figueiredo IB, Scariot A (2007) Ethnobotany and effects of harvesting on the population ecology of *Syngonanthus nitens* (Bong.) Ruhland (Eriocaulaceae), a NTPF from Jalapão region, Central Brazil. *Economic Botany* **61**, 73-85
- Schütz W, Rave G (1999) The effect of cold stratification and light on the seed germination of temperate sedges (*Carex*) from various habitats and implications for regenerative strategies. *Plant Ecology* **144**, 215-230
- Simpson RL (1989) Seed banks: general concepts and methodological issues. In: Leck MA, Parker VT, Simpson RL (Eds) *Ecology of Soil Seed Banks*, Academic Press, London, pp 3-8
- Specht CE, Keller ERJ (1997) Temperature requirements for seed germination in species of the genus *Allium* L. *Genetic Resources and Crop Evolution* **44**, 509-517
- Takaki M (2001) New proposal of classification of seeds based on forms of phytochrome instead of photoblastism. *Revista Brasileira de Fisiologia Vegetal* **13**, 104-108
- Teixeira AM (1987) Sempre-vivas: Folclore e verdade. *Ciência Hoje* **5**, 14-15
- Thompson PA (1973) Geographical adaptation of seeds. In: Heydecker W (Ed) *Seed Ecology*, Butterworths, London, pp 31-58

- Thompson K, Grime JP** (1983) A comparative study of germination responses to diurnally-fluctuating temperatures. *Journal of Applied Ecology* **20**, 141-156
- Thompson K** (1993) Seeds. In: Hendry GAF, Grime JP (Eds) *Methods in Comparative Plant Ecology*, Chapman and Hall, UK, pp 176-205
- Thompson K** (2000) The functional ecology of soil seed banks. In: Fenner M (Ed) *The Ecology of Regeneration in Plant Communities*, CAB International Wallingford, UK, pp 215-236
- Tomlinson PB** (1969) Comelinales-Zingiberales. In: Metcalfe, Chalk CR (Eds) *Anatomy of the Monocotyledons*, Clarendon Press, Oxford, pp 295-421
- Vázquez-Yanes C, Orozco-Segovia A** (1993) Patterns of seed longevity and germination in the tropical rainforest. *Annual Review of Ecology and Systematics* **24**, 69-87
- Venable DL, Brown JS** (1988) The selective interactions of dispersal, dormancy and seed size as adaptations for reducing risk in variable environments. *The American Naturalist* **131**, 360-384
- Villalobos AE, Peláez DV** (2001) Influences of temperature and water stress on germination and establishment of *Prosopis caldenia* Burk. *Journal of Arid Environments* **49**, 321-328
- Wanderley MGL** (1992) Estudos taxonômicos no gênero *Xyris* L. (Xyridaceae) da Serra do Cipó, Minas Gerais, Brasil. São Paulo. PhD Thesis, Instituto de Biociências de São Paulo, 300 pp
- Westoby M, Jurado E, Leishman M** (1992) Comparative evolutionary ecology of seed size. *Trends in Ecology and Evolution* **7**, 368-372