Diversity of germination strategies and seed dormancy in herbaceous species of *campo rupestre* grasslands

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**Running title:** Germination strategies in tropical grasslands

**Abbreviations:** MGT: Mean Germination Time; $\bar{E}$: germination synchrony; GLM: Generalized Linear Models.
Abstract
The effects of fire on the vegetation vary across continents. However, in Neotropical fire-prone grasslands, the relationship between fire and seed germination is still poorly understood, while their regeneration, especially after strong anthropogenic disturbance, is challenging for their conservation. In the present study, we assessed diversity of germination strategies in 15 dominant herbaceous species from Neotropical altitudinal grasslands (locally known as campos rupestres). We exposed seeds to several fire-related treatments. We also compared germination between regularly and post-fire fruiting species. Finally, we investigated the diversity of dormancy classes aiming at better understanding the biogeography and phylogeny of seed dormancy. Germination strategies varied among families. Velloziaceae and Xyridaceae produced non-dormant, fast-germinating seeds. Cyperaceae and Poaceae showed an extremely low or null germination, due to a high proportion of unviable or embryoless seeds. The seeds of campo rupestre grasslands are fire-resistant, but there is no evidence that fire triggers germination in this fire-prone ecosystem. Although heat and charred wood did not promote germination, smoke enhanced germination in one grass species, and decreased the mean germination time and improved synchrony in Xyridaceae and Velloziaceae. Fire had a positive effect on post-fire regeneration by stimulating fruit set in some Cyperaceae and Poaceae species. These species produced faster-germinating seeds with higher germination percentage and synchrony compared to regularly fruiting Cyperaceae and Poaceae species. This strategy of dispersion and regeneration seems to be an alternative to the production of seeds with germination triggered by fire. Physiological dormancy is reported for the first time in several clades of Neotropical plants. Our data help advance the knowledge on the role of fire in the regeneration of Neotropical grasslands.
Key-words: Fire-related germination; Neotropical grasslands; physiological dormancy; temperature fluctuation.
INTRODUCTION

In fire-prone environments plants show adaptive strategies that enable them to persist or thrive in the face of recurrent fires (Bond & Keeley 2005). Fire-resistant or fire-persistent species show two different regeneration strategies. “Resprouters” (Clarke et al. 2013) recover from fire via vegetative regeneration, whereas “seeders” germinate from the seed bank or from newly dispersed seeds (Whelan 1995, Bond & Van Wilgen 1996, Hoffmann 1998; Keeley & Fotheringham 2000; Pausas et al. 2004; Bond & Keeley 2005).

In the case of obligate seeders (species which are not able to resprout after fire), regeneration from seeds is the only way to recover from this kind of disturbance (Keeley 1986, Whelan 1995). Hence, germination in these species is expected to be triggered by fire-related cues. The persistence of seeders at a site depends on: (1) their ability to produce seeds during the inter-fire period, (2) seed survival probability during fire, and (3) the degree to which recruitment is enhanced by fire (Pausas et al. 2004). Several species in fire-prone environments have part of their recruitment process restricted to the first year after fire (Bond & Van Wilgen 1996), because growth and reproduction are stimulated by fire-related cues. In those cases, germination is usually triggered by heat, smoke, or charred wood, as direct consequences of fire include increase in aboveground temperatures and smoke production (Bond & Keeley 2005; Keeley & Fotheringham 2000).

However, fire effects on vegetation vary across continents (Lehmann et al. 2014). In Neotropical grasslands most species are perennial and resprout after fire (Hoffmann 1998). However, germination in herbaceous species is poorly documented and, hence, the relationship between fire and germination in Neotropical species should be further studied. Fire-stimulated flowering and fruit set is also pointed out as another alternative strategy; it is a mechanism of recruiting seedlings after fire (Bond & Van Wilgen 1996, Bond and Keeley
Flowering occurs just after fire on sprouts and allows producing a large amount of seeds able to germinate in the first or second years after fire.

The relationship between germination and fire is well documented in fire-prone environments, such as Mediterranean vegetation (Keeley & Fotheringham 1997; Keeley & Bond 1997; Keeley & Fotheringham 1998, Pérez-Fernández & Rodríguez-Echeverría 2003; Moreira et al. 2010, Santana et al. 2013), Australian vegetation (Williams et al. 2003, 2005), African savannas (Dayamba et al. 2008, 2010), and African fynbos (Keeley & Bond 1997).

However, the effects of fire on the germination of herbaceous species in Neotropical grasslands and the effects of fire-related cues remain poorly understood (Ribeiro et al. 2013, Ribeiro & Borghetti 2014). In Neotropical grasslands, such as campos rupestres, some studies assessed the effect of light and temperature on germination. However, no study has addressed the impact of fire on germination (but see Fichino et al. 2012).

*Campos rupestres*, a part of the Cerrado biome, are species-rich grasslands that grow on quartzite-derived soils at altitudes between 800 and 2,000 m a.s.l. They constitute a mosaic of grasslands and scattered rocky outcrops dominated by ericoid, sclerophyllous evergreen shrubs and sub-shrubs (Alves & Kolbek 2010; Le Stradic et al 2014; Appendix 1) that grow on shallow, highly acid, nutrient-poor soils (Benites et al. 2007; Le Stradic 2012). *Campos rupestres* harbour high floristic diversity (4,000 estimated species) with one of the highest levels of endemism found in Brazil (Alves & Kolbek 2010; Echternacht et al. 2011; Giulietti et al. 1997). Like all savannas, the Cerrado is subjected to recurrent fires (Simon et al. 2009), which is an important factor that regulates vegetation dynamics in these ecosystems (Bond et al. 2005; Cochrane 2009). Simon et al. (2009) have argued that fire acts as an ecological tool in the Cerrado, as it maintains open some types of vegetation such as the campos rupestres.

Seed dormancy evolved several times in species that occur in seasonal environments, and it prevents seedlings from establishing under unfavourable conditions (Baskin & Baskin 2005).
There has been some progress in understanding the germination of *campo rupestre* plants. However, we still need more studies on the phylogeny of seed dormancy, in order to understand the dynamics of adaptive strategies in its flora and the relationship between dormancy and plant traits (Jurado & Flores 2005, Baskin & Baskin 2014). Seed dormancy in many woody plants of *campos rupestres* appears to be phylogenetically conserved (Gomes et al. 2001; Silveira & Fernandes 2006). Nevertheless, the causes of dormancy in herbs that occur in *campos rupestres* and the historical forces driving its evolution are poorly known (Garcia et al. 2011).

The aim of the present study was to assess the diversity of germination strategies in herbs that occur in *campos rupestres*. In fire-prone environments, plant and vegetation responses to fire differ among continents (Lehmann et al. 2014). Hence, studying seed germination ecology in *campos rupestres* will allow comparisons with African and Australian grasslands. We described the germination ecology of 15 dominant species under several conditions and tested whether seeds respond positively to fire-related cues. We also assessed seed germination in four post-fire fruiting species and compared their germination behaviour with that of regularly fruiting species. We report some insights on the seed dormancy of the studied species and discuss our results in the context of results obtained in other fire-prone environments in different biogeographic regions.

**MATERIAL AND METHODS**

**Seed collection**

The present study was carried out at Serra do Cipó (19°17' S; 43°33' W), in the southern part of the Espinhaço Mountain Range (state of Minas Gerais, south-eastern Brazil), where *campos rupestres* (rocky/rupestrian grasslands) is the dominant vegetation. The climate is classified as Cwb, with a cool dry season (from May to October) and a warm rainy season.
(from November to April), according to the Köppen system (Köppen 1900). The average annual rainfall is 1,622 mm and the average annual temperature is 21.2 °C (Madeira & Fernandes 1999). Natural fires occur at the end of the dry season, whereas man-made fires are frequent in the mid dry season.

Fifteen dominant species from campos rupestres were selected from a phytosociological study (Le Stradic 2012) based on seed availability. Our sample was composed of species that produce seeds regularly (i.e. every year), including five Cyperaceae: Lagenocarpus tenuifolius, Lagenocarpus alboniger, Rhynchospora ciliolata, R. consanguinea, and R. riedeliana; two Poaceae: Aristida torta and Echinolaena inflexa; four Velloziaceae: Vellozia epidendroides, V. caruncularis, V. resinosa, and V. variabilis; two Xyridaceae: Xyris obtusiuscula and X. pilosa; and two Asteraceae: Richterago arenaria and Lessingianthus linearifolius (Appendix 2). All studied species are perennial hemicryptophytes except for V. variabilis, which is nanophanerophyte, and have abiotic seed dispersal. All species resprout after fire (Le Stradic 2012). Seeds were manually collected from randomly selected individuals of different populations (n > 50 per species) in unburned areas (for at least the past five years) during the fruit set peak of 2010. For Poaceae, we used the entire diaspore without removing accessory structures, such as lemma and palea (Baskin et al. 2006). We will henceforth refer to the achenes of Asteraceae as seeds.

To compare seed germination between regularly and post-fire fruiting species, we analysed seed germination in four additional resprouter species, which fruit only after fire (Appendix 3). We collected from a recently burned area (fire in August 2011) seeds of two Cyperaceae: Bulbostylis emmerichiae and B. paradoxa; and two Poaceae: Homolepis longispicula and Paspalum pectinatum. Nearly two weeks after fire those plants had already resprouted and produced flowers (Le Stradic, personal observation). Seeds from Cyperaceae and Poaceae were collected in December 2011 and January 2012, respectively.
Germination experiments

We assessed the effects of temperature, dry heat, smoke water, charred wood, and soil on seed germination. In the soil treatment, seeds were sown on a 1-cm deep layer of soil collected from randomly picked locations in the natural grasslands where the species occur. We expected the soil to decrease the imbibition rate by decreasing water availability. In the dry heat treatment, seeds were exposed to 100 °C for 5 min in an oven prior to sowing (González-Rabanal & Casal 1995; Keeley & Bond 1997; Ribeiro et al. 2013), in accordance with data obtained for the Cerrado (Miranda et al. 1993; Ribeiro et al. 2013). In the smoke water treatment, smoke was obtained from burning leaves and wooden stems and funnelled through a hose into a distilled water sample. First-day seeds were watered with a 1:10 diluted smoked water solution. From the second day on, seeds were watered with distilled water (Clarke & French 2005). In the charred wood treatment, seeds were watered with 10 ml of an aqueous suspension of charred wood (González-Rabanal & Casal 1995; Pérez-Fernández & Rodríguez-Echeverría 2003). This suspension was obtained from the combustion of dried plant material (i.e. hay of grasses and forbs) collected in grasslands so that it contained representative species of campos rupestres. An initial biomass of 408 g was burned, resulting in 50 g of charred wood, and then sieved (2mm). The charred wood was diluted with distilled water to a concentration of 10 g of charred wood per litre.

Seeds were put to germinate in Petri dishes (five replicates of 20 seeds per treatment), covered with filter paper, and moistened with Nistatina® suspension to prevent fungi growth. Seeds were placed in germination chambers kept at a constant temperature of 25 °C under a 12-h photoperiod, because these are optimum conditions for the germination of campo rupestre plant species. As an additional treatment, seeds were also exposed to fluctuating temperatures between 15 °C and 25 °C and between 20 °C and 30 °C, based on a 12-h
photoperiod (with the highest temperature corresponding to daytime). Seeds were exposed to 27 μmol m$^{-2}$ s$^{-1}$ light incidence, because small-sized seeds of *campos rupestres* herbs are light-demanding (Abreu & Garcia 2005; Oliveira & Garcia 2012; Mota & Garcia 2013; Silveira *et al.* 2013). All seeds were monitored for 30 consecutive days (Baskin *et al.* 2006) to make our data comparable to other studies (Baskin & Baskin 2014). Germination was checked every 24 h and germination was determined through radicle emergence.

After germination tests, seed viability was assessed in all species through seed dissection procedures followed by a tetrazolium test applied to fresh seeds. Seeds that did not germinate were cut and placed in a 1% solution of 2,3,5-triphenyl-2H-tetrazolium chloride (TTC) for 48 h under dark conditions in a chamber at 25 °C (Peters & Lanham 2005).

**Germination of regularly and post-fire fruiting species**

Four species did not produce fruits regularly but had massive fruit production right after fire: *Bulbostylis emmerichiae*, *B. paradoxa*, *Homolepis longispicula*, and *Paspalum pectinatum*. Seeds of these post-fire fruiting species were placed in germination chambers (five replicates of 20 seeds/species) kept at a constant temperature of 25°C, in a 12-h photoperiod. Germination behaviour of these Poaceae and Cyperaceae seeds was then compared to the germination behaviour of Poaceae and Cyperaceae seeds of regularly fruiting species exposed to the same conditions (i.e. constant temperature of 25 °C and a 12-h photoperiod).

**Determination of seed dormancy classes**

In the present study, seed dormancy was defined as the absence of germination in viable seeds subjected to favourable germination conditions (Hilhorst 2011). Seed dormancy classes followed Baskin and Baskin (2004). Physical dormancy implies that the seed or fruit
coat is impermeable to water. To determine whether diaspores were water impermeable, four
replicates of 25 seeds (100 seeds for Xyridaceae species) were weighed on a digital balance,
soaked in distilled water for 72h at room temperature, and then reweighed. Seed permeability
was determined by the increase in seed mass between dry and soaked seeds. We dissected dry
seeds under a stereomicroscope to determine embryo developmental patterns and infer on
morphological and morphophysiological dormancy (Baskin & Baskin 2004).

Statistical analyses

For each replicate, we calculated final germination percentage, mean germination time
(MGT), and germination synchrony ($E$) (Ranal & Santana 2006), using the formula:

$$MGT = \sum_{i=1}^{k} n_i t_i / \sum_{i=1}^{k} n_i$$

where $t_i$ is the time from the start of the experiment to the $i^{th}$ observation, $n_i$ is the number of
germinated seeds at time $i$ (not the accumulated number), and $k$ is the last time of
germination. And the formula:

$$E = -\sum_{i=1}^{k} f_i \log_2 f_i \text{ with } f_i = n_i / \sum_{i=1}^{k} n_i$$

where $f_i$ is the relative frequency of germination, $n_i$ is the number of germinated seeds on
day $i$, and $k$ is the final day of observation. Low $E$ values indicate more synchronized
germination and high $E$ values indicate less synchronized germination.

We used generalized linear models (GLM), with quasi-binomial distribution and a
logit link function to compare the final germination percentage among treatments (25°C,
15°C/25°C, 20°C/30°C, soil, heat, smoke water, and charred wood) for the species: A. torta,
L. linearifolius, V. caruncularis, V. epidendroides, V. resinosa, V. variabilis, X. obtusiuscula,
and X. pilosa (other species showed low or no germination). We used a GLM with a gamma
distribution and an inverse link function to compare mean germination time among treatments for the same species. To compare germination synchrony among treatments per each species, we used simple analyses of variance (ANOVA), followed by post hoc tests (Tukey test), in which germination synchrony was treated as the dependent variable and treatment as the factor. Normality and homoscedasticity assumptions were checked and a square root transformation was applied whenever necessary (Sokal & Rohlf 1998). In addition, we used a GLM with a quasi-binomial distribution and a logit link function to test for differences in the percentage of viable and embryoless seeds among species.

We compared the final germination percentage between regularly and post-fire fruiting species with a GLM (quasi-binomial distribution and logit link function). We tested for differences in mean germination time among species using a GLM (gamma distribution and inverse link function) and used a t-test to compare germination synchrony between the two treatments. At the species level, we compared the final germination percentage of all species (regularly fruiting species vs. post-fire fruiting species) with a GLM, using a quasi-binomial distribution and logit link function. We also compared mean germination time among species with a GLM (gamma distribution and inverse link function). We tested for differences in germination synchrony among species with an ANOVA, followed by post hoc Tukey tests, in which germination synchrony was treated as the dependent variable and species as the factor. Normality and homoscedasticity assumptions were previously checked and a square root transformation was applied whenever necessary.

We analysed seed coat permeability with paired t-tests, in order to test for differences in weight gain between dried and soaked seeds. All analyses were carried out in R 2.9.1 (R Development Core Team 2010).

RESULTS
Seed germination requirements and effects of fire-related cues

Seeds of *E. inflexa*, *L. alboniger*, *L. tenuifolius*, *R. ciliolata*, *R. consanguinea*, *R. riedeliana*, and *R. arenaria* showed low or no germination regardless of the treatment (Table 1). *Vellozia caruncularis* and *V. variabilis* had high germination percentage (>75% and >88%, respectively) regardless of the treatment (Table 1). *Vellozia epidendroides*, *V. resinosa*, and *X. pilosa* had high germination percentages at 25 °C, but experienced a germination decrease at temperatures fluctuating between 15 °C and 25 °C. *Xyris obtusiuscula* and *A. torta* were not affected by fluctuating temperatures (Table 1). The soil treatment had a negative effect on the germination of *L. linearifolius*, *V. epidendroides*, and *V. resinosa* (Table 1).

The responses of seeds to fire-related cues were idiosyncratic. Dry heat had no effect on germination percentage in any species, except for *A. torta* (Table 1). *Aristida torta* showed its highest germination percentage (21%) in the smoke water treatment, whereas heat decreased its germination to 1% (Table 1). No fire-related cues affected germination percentage in *L. linearifolius* (Table 1). Charred wood affected germination percentage negatively in *V. epidendroides*, *X. obtusiuscula*, and *X. pilosa*.

Overall, temperatures fluctuating between 15 °C and 25 °C and between 20 °C and 30 °C increased the mean germination time of all species (Table 2). They also increased the germination synchrony in *V. epidendroides* and *X. pilosa* (Table 3). Soil treatment reduced the mean germination time of *V. variabilis* (Table 2). In most species, dry heat had no effect on mean germination time, but it reduced moderately mean germination time in *V. epidendroides* and *V. resinosa* (Table 2). Charred wood increased mean germination time and synchrony in *V. resinosa* (Table 1, Table 2). In addition, smoked water improved mean germination time in *X. pilosa* (Table 2) and increased germination synchrony in *V. epidendroides*, *V. resinosa*, and *X. pilosa* (Table 3).
Viability

*Aristida torta, L. alboniger, R. ciliolata, L. linearifolius*, and *R. arenaria* had over 50% of embryoless seeds (the percentage of embryoless seeds differed significantly among species; $F = 88.76, P < 0.001$) (Table 4). In Xyridaceae and Velloziaceae, the percentage of embryoless seeds was often below 10%. *Echinolaena inflexa, L. alboniger, R. ciliolata,* and *R. arenaria* exhibited seed viability below 10%. Seed viability in *A. torta, R. riedeliana, L. tenuifolius, R. consanguinea,* and *L. linearifolius* ranged from 10% to 42%, whereas in Xyridaceae and Velloziaceae seed viability was above 85% (the percentage of viable seeds differed significantly among species; $F = 75.81, P < 0.001$) (Table 4).

Germination of regularly and post-fire fruiting species

Among post-fire fruiting species, the germination percentage of *H. longispicula, B. emmerichiae,* and *B. paradoxa* was above 75%, whereas *P. pectinatum* showed lower germination percentage ($F = 28.08, P < 0.001$, Figure 1). Both post-fire fruiting Poaceae (*H. longispicula* and *P. pectinatum*) showed higher germination percentage than regularly fruiting Poaceae ($F = 30.37, P < 0.001$). The same pattern was observed in Cyperaceae, in which germination percentages were higher in the post-fire fruiting species (*B. emmerichiae,* and *B. paradoxa*) than in regularly fruiting species ($F = 600.85, P < 0.001$).

The two Poaceae species (*H. longispicula* and *P. pectinatum*) had shorter mean germination time than *B. emmerichiae, B. paradoxa,* and *A. torta* ($F = 33.46, P < 0.001$, Figure 1). *Paspalum pectinatum* showed higher synchrony than the three other post-fire fruiting species ($F = 16.87, P < 0.001$), but this could be an artefact caused by the lower germination rate of this species (Figure 1).

Determination of seed dormancy classes
In eight out of 15 species, seed germination percentages were below 10% under suitable germination conditions (Table 1). *Echinolaena inflexa, L. alboniger, R. ciliolata,* and *R. arenaria* produced high percentages of unviable seeds and embryoless seeds (Table 4). Thus, in these four species, lack of germination is attributed to low seed quality, and no safe conclusions on seed dormancy can be drawn from these species. Seeds of *A. torta, L. tenuifolius, R. consanguinea,* and *R. riedeliana* were considered to have at least some degree of dormancy, with percentages ranging from 68 to 100% (Table 4). Although 29% of the *X. obtusiuscula* seeds germinated, nearly 67% of its seeds were viable (Table 4). Hence, the seeds of these five species were considered primarily dormant.

The increase in weight after soaking seeds in tap water ranged from 6.2 to 217%. This increase in seed weight was significant for all studied species (and nearly significant for *V. epidendroides*, Appendix 4). Hence, all species produced water-permeable seed coats and did not present physical dormancy. Mature seeds of the five dormant species (*A. torta, L. tenuifolius, R. consanguinea, R. riedeliana,* and *X. obtusiuscula*) produced differentiated embryos that occupied most of the seed cavity. These seeds are, therefore, physiologically dormant (PD).

**DISCUSSION**

Our results show that herbaceous plants of the *campos rupestres* have a large diversity of seed germination strategies. There were clear interspecific and interfamily differences in germination. Seven out of 15 species of Poaceae and Cyperaceae had only sporadic germination and produced high percentages of unviable or dormant seeds. We could not expect responses to fire-related cues from those species (*E. inflexa, L. alboniger, L. tenuifolius, R. ciliolata, R. consanguinea, R. riedeliana,* and *R. arenaria*), due to their low viability, our discussion is thus focused on the other group of species that produced non-
dormant, fast-germinating seeds.

Our results on fluctuating temperatures corroborate other studies carried out in Cerrado and campo rupestre species, which showed that alternating temperatures either decrease or have no effect on germination (Velten & Garcia 2005; Silveira et al. 2013). Seeds of L. linearifolius, Vellozia, and Xyris are non-dormant and germinated without undergoing pre-germination treatments. Our germination results using campo rupestre soil suggest that some species, such as L. linearifolius, V. epidendroides, and V. resinosa, might be particularly sensitive to the imbibition phase. Water imbibition is crucial to seed germination: when a dry seed enters the soil, imbibition occurs prior to germination and the seed must absorb enough water to germinate. However, the critical hydration level is species-specific (Hadas & Russo 1974).

Seed germination of shrubs and trees of Mediterranean-like ecosystems or savannas can be stimulated by fire-related cues, such as charred wood or dry heat exposure (Keeley & Bond 1997; Pérez-Fernández & Rodríguez-Echeverría 2003; Dayamba et al. 2008; Ribeiro et al. 2013). However, our results do not support the hypothesis that fire-related cues trigger germination in Neotropical herbs. As already observed in herbaceous species of savannas (Dayamba et al. 2008, 2010; Fichino et al. 2012) no fire-related cue had a marked effect on seed germination. Unlike Mediterranean species, germination in X. pilosa, X. obtusiuscula, V. epidendroides, and V. resinosa was inhibited or decreased by charred wood. However, smoke stimulated germination in A. torta, decreased the mean germination time, and increased germination synchrony in most of the studied species.

In our study, heat did not improve seed germination in herbaceous species. Heat-stimulated seeds exhibit physical dormancy imposed by a dense palisade tissue (Keeley & Fotheringham 2000; Ribeiro et al. 2013). Heat disrupts this tissue, which increases water permeability. All studied species have water-permeable seed coats and lack physical
dormancy, which may be restricted to some clades, such as Fabaceae (Gomes et al. 2001; Silveira & Fernandes 2006). Heat is a direct effect of fire (Keeley & Fotheringham 2000).

Other combinations of temperatures and exposure times should be tested to further assess the role of heat on the germination of campo rupestre plants.

In our study, the effects of charred wood and smoke were contradictory, whereas in the Mediterranean region, smoke and charred wood increased germination (Keeley & Fotheringham 1998; Pérez-Fernández & Rodríguez-Echeverría 2003). The first hypothesis to explain those differences is that the chemical compounds produced by smoke and charred wood are different and, thus, have different effect on germination. The second hypothesis is that the studied seeds need time to become sensitive to fire-related cues (e.g., following wet–dry cycles and dry periods after ripening (Long et al. 2011a; Long et al. 2011b). The third hypothesis is that seed germination triggered by smoke carrying karrikinolide compounds (Bradshaw, Dixon, Hopper, Lambers, & Turner, 2011; Flematti, Ghisalberti, & Dixon, 2004) is not a fire-adapted plant trait (Bradshaw et al. 2011). Indeed, organic matter decay was already pointed out as the first driver in the development of smoke-mediated germination (Bradshaw et al. 2011).

Despite the lack of evidence of fire-induced germination, fire might still play an important role in the regeneration of plant communities in campos rupestres. Firstly, all but one species showed high tolerance to high temperatures, which suggests that fire-tolerance is common in campo rupestre species similar to other fire-prone grasslands in southern and central Brazil (Overbeck et al. 2005; Overbeck & Pfadenhauer 2007; Fichino et al. 2012). Secondly, post-fire fruiting species had high, fast, and synchronous germination, which indicates an adaptive advantage of regeneration after fire. Indeed, regularly fruiting Poaceae and Cyperaceae had low or null germination rate, whereas post-fire fruiting Poaceae and Cyperaceae species had high germination rate and short mean germination time. The massive
flower production just after fire favours cross-breeding, which promotes vigorous seedlings with a wide habitat tolerance (Lamont & Wiens 2003). Moreover, fire decreases competition and increases resource availability (i.e. nutrients, light, and space). Species that produce seeds only after fire may have been selected, because relaxed interspecific competition after fire is expected to increase their likelihood of establishment (Santana et al. 2013). Like seeders, our four post-fire fruiting species (resprouters) produced several viable seeds after fire. This fact may indicate that the ultimate role of seeds in resprouter species is dispersal instead of survival. However, our results should be interpreted with caution, as we did not test for a phylogenetical signal in the comparison between regularly and post-fire fruiting species.

On the other hand, all studied species are resprouters, which suggests that resprouting is the dominant mechanism for regeneration after fire in campos rupestres (Simon et al. 2009). This may lead to lower investment in sexual reproduction and explains why many of the studied species, especially the Poaceae and Cyperaceae, had almost no germination (Paula & Pausas 2008). Resprouters represent a large group of Neotropical fire-prone communities (Hoffmann 1998; Overbeck & Pfadenhauer 2007) Resprouting provides an alternative to the establishment from seeds after fire, and allows the plant to persist in the environment (Hoffmann 1998; Fidelis et al. 2010). Our results indicate that some resprouters from campos rupestres produce many embryoless or unviable seeds, especially wind-pollinated species (Cyperaceae and Poaceae). This pattern seems to be widespread in Cyperaceae, Asteraceae, and Poaceae (Leck & Schutz 2005; Overbeck & Pfadenhauer 2007; Velten & Garcia 2005).

Low fecundity among resprouters in comparison to non-sprouters can be explained by resource limitation, breeding system limitation, and genetic load (Lamont et al. 2011; Lamont & Wiens 2003). Conversely, the Xyridaceae and Velloziaceae, which are also resprouter species, showed a high germination rate, regardless of the treatment. Hence, this pattern is not applicable to all families.
Our data suggest that populations of *A. torta*, *X. obtiuscula*, *L. tenuifolius*, *R. consanguinea*, and *R. riedeliana* produce physiologically dormant seeds (*sensu* Baskin & Baskin 2004). Physiological dormancy occurs in most Cyperaceae (Leck & Schutz 2005) and Poaceae species (Baskin & Baskin 2014). However, despite recent reports on secondary dormancy (Garcia *et al.* 2011), there were no reports of primary dormancy in Xyridaceae. Seed dormancy in Poaceae is a consequence of chemical inhibition or mechanical resistance of glumes, lemmas, and palea (Gasque & García-fayos 2003; Ma *et al.* 2010). To the best of our knowledge, this is the first record of primary dormancy in Cyperaceae, Poaceae, and Xyridaceae species of *campos rupestres*. Further efforts to study other species are especially important to shed light on the relationships between seed dormancy and species life history (Jurado & Flores 2005).

In summary, in contrast to other fire-prone vegetation types, our study shows that seed germination of herbaceous species of *campos rupestres* is unresponsive to fire-related cues. These contrasting results may be related to the evolutionary history of plants in fire-prone environments in different continents (Lehmann *et al.* 2014). Our study also shows marked differences in germination among families. However, fire may play an important role in regeneration in *campos rupestres*. Most studied species are fire-tolerant and, at least in Cyperaceae and Poaceae, post-fire fruiting species germinate quicker and more synchronously than regularly fruiting species. Finally, we report new records of physiological dormancy in many clades, which contributes to the understanding of phylogenetic and biogeographic distribution of seed dormancy (Baskin & Baskin 2014). The relationship between germination and fire seems quite different in Neotropical grasslands compared to African or Mediterranean fire-prone environments. We hope our data improve cross-continental comparisons of fire-related cues on seed germination and provide important information for fire management of this threatened ecosystem.
ACKNOWLEDGEMENTS

We thank William Bond and Gregory Mahy for their suggestions on the text, Kolo D Wamba who revised the English and anonymous reviewers for their comments to improve the manuscript. This work was supported by the Conselho Nacional de Pesquisa [CNPq 561883/2010-6]; Fundação do Amparo a Pesquisa de Minas Gerais [Fapemig APQ-04105-10], Natural Reserva Vellozia and the Ministère Français des affaires étrangères et européennes [EGIDE 2009/657176K].

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Le Stradic S. (2012) Composition, phenology and restoration of *campo rupestre* mountain grasslands. PhD dissertation, Departement of Sciences and Agrosciences, Université
d’Avignon et des Pays de Vaucluse, Avignon, France and Department of General Biology, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil: 322pp.


Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ 

research, 3rd edition. WH Freeman, New York, USA.

19, 753–761.


dormancy of six legumes of tropical eucalypt savannas in north-eastern Australia.

Table 1. Germination percentage (mean ± standard error) for graminoid and forb species of *campos rupestres* grasslands in the various treatments. GLM procedures (with quasibinomial distribution) were performed for *A. torta, L. linearifolius, V. caruncularis, V. epidendroides, V. resinosa, V. variabilis, X. obtusiuscula* and *X. pilosa*. Lack of data means no germination under this specific condition. Within a species, treatment values with different lower case letters were significantly different according to the GLM results.

<table>
<thead>
<tr>
<th>Species</th>
<th>Control</th>
<th>15°C/25°C</th>
<th>20°C/30°C</th>
<th>Charred wood</th>
<th>Water smoke</th>
<th>Dry heat</th>
<th>Soil</th>
<th>GLM</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aristida torta</em></td>
<td>9.00 ± 2.10</td>
<td>5.00 ± 3.06</td>
<td>10.00 ± 3.95</td>
<td>7.00 ± 2.24</td>
<td>21.00 ± 6.94</td>
<td>1.00 ± 1.12</td>
<td>9.00 ± 4.81</td>
<td>F=3.45 **</td>
</tr>
<tr>
<td><em>Echinolaena inflexa</em></td>
<td>-</td>
<td>-</td>
<td>1.00 ± 1.12</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Lagenocarpus alboniger</em></td>
<td>-</td>
<td>-</td>
<td>1.00 ± 1.12</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Lagenocarpus tenuifolius</em></td>
<td>4.00 ± 2.10</td>
<td>1.00 ± 1.12</td>
<td>-</td>
<td>1.00 ± 1.12</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Rhynchospora ciliolata</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.00 ± 1.12</td>
<td>-</td>
<td>-</td>
<td>1.00 ± 1.12</td>
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</tr>
<tr>
<td><em>Rhyzchospora consanguinea</em></td>
<td>-</td>
<td>3.00 ± 2.24</td>
<td>1.00 ± 1.12</td>
<td>-</td>
<td>-</td>
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<td>-</td>
</tr>
<tr>
<td><em>Lessingianthus linearifolius</em></td>
<td>41.00 ± 1.12</td>
<td>52.00 ± 5.18</td>
<td>33.00 ± 10.69</td>
<td>24.00 ± 4.11</td>
<td>25.00 ± 6.12</td>
<td>37.00 ± 10.69</td>
<td>7.00 ± 3.79</td>
<td>F=5.71 ***</td>
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<tr>
<td><em>Richterago arenaria</em></td>
<td>-</td>
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<td>-</td>
<td>1.00 ± 1.12</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Vellozia caruncularis</em></td>
<td>84.00 ± 4.11</td>
<td>86.00 ± 6.22</td>
<td>80.00 ± 6.85</td>
<td>90.00 ± 3.95</td>
<td>82.00 ± 3.79</td>
<td>75.00 ± 6.37</td>
<td>86.00 ± 7.37</td>
<td>F=0.87 NS</td>
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<tr>
<td><em>Vellozia epidendroides</em></td>
<td>83.00 ± 3.79</td>
<td>32.00 ± 1.37</td>
<td>78.00 ± 7.20</td>
<td>9.00 ± 2.44</td>
<td>85.00 ± 3.06</td>
<td>85.5 ± 1.63</td>
<td>27.5 ± 6.79</td>
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<td><em>Vellozia resinosa</em></td>
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<td>37.00 ± 4.63</td>
<td>93.50 ± 1.12</td>
<td>90.00 ± 3.95</td>
<td>94.00 ± 4.47</td>
<td>86.00 ± 3.14</td>
<td>30.00 ± 5.86</td>
<td>F=43.28 ***</td>
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<tr>
<td><em>Vellozia variabilis</em></td>
<td>88.00 ± 3.35</td>
<td>90.00 ± 1.77</td>
<td>92.00 ± 2.85</td>
<td>97.00 ± 3.35</td>
<td>97.00 ± 2.24</td>
<td>96.00 ± 2.09</td>
<td>95.00 ± 2.50</td>
<td>F=1.75 NS</td>
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<tr>
<td><em>Xyris obtusiuscula</em></td>
<td>29.00 ± 8.95</td>
<td>28.5 ± 6.94</td>
<td>10.00 ± 2.34</td>
<td>2.00 ± 1.37</td>
<td>41.00 ± 8.91</td>
<td>27.00 ± 6.02</td>
<td>-</td>
<td>F=9.79 ***</td>
</tr>
<tr>
<td><em>Xyris pilosa</em></td>
<td>79.50 ± 5.03</td>
<td>28.5 ± 4.29</td>
<td>74.50 ± 5.55</td>
<td>15.00 ± 3.54</td>
<td>72.00 ± 7.20</td>
<td>71.00 ± 6.03</td>
<td>-</td>
<td>F=38.72 ***</td>
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</table>
Table 2. Mean germination time [MGT in days (mean ± standard error)] for graminoid and forb species of *campo rupestre* grasslands in the various treatments. GLM procedures (with Gamma distribution) were performed for *A. torta, L. linearifolius, V. caruncularis, V. epidendroides, V. resinosa, V. variabilis, X. obtusiuscula* and *X. pilosa*. Lack of data means no germination under this specific condition. Within a species, treatment values with different lower case letters were significantly different according to the GLM results.

<table>
<thead>
<tr>
<th>Species</th>
<th>Control</th>
<th>15°C/25°C</th>
<th>20°C/30°C</th>
<th>Charred wood</th>
<th>Water smoke</th>
<th>Dry heat</th>
<th>Soil</th>
<th>GLM</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aristida torta</em></td>
<td>12.16 ± 1.34&lt;sup&gt;a&lt;/sup&gt;</td>
<td>22.66 ± 5.06&lt;sup&gt;b&lt;/sup&gt;</td>
<td>19.62 ± 3.25&lt;sup&gt;a&lt;/sup&gt;</td>
<td>16.12 ± 3.45&lt;sup&gt;a&lt;/sup&gt;</td>
<td>9.44 ± 1.09&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6.00 ± 0.00&lt;sup&gt;a&lt;/sup&gt;</td>
<td>15.12 ± 3.84&lt;sup&gt;a&lt;/sup&gt;</td>
<td>F=3.45 ***</td>
</tr>
<tr>
<td><em>Echinolaena inflexa</em></td>
<td>-</td>
<td>-</td>
<td>25.00 ± 0.00</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Lagenocarpus alboniger</em></td>
<td>-</td>
<td>-</td>
<td>26.00 ± 0.00</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Lagenocarpus tenuifolius</em></td>
<td>-</td>
<td>29.66 ± 0.28</td>
<td>30.00 ± 0.00</td>
<td>-</td>
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</tr>
<tr>
<td><em>Rhynchospora ciliolata</em></td>
<td>-</td>
<td>-</td>
<td>29.00 ± 0.00</td>
<td>-</td>
<td>20.00 ± 0.00</td>
<td>-</td>
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<tr>
<td><em>Rhynchospora consanguinea</em></td>
<td>-</td>
<td>-</td>
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<td>-</td>
<td>-</td>
<td>23.00 ± 0.00</td>
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<tr>
<td><em>Rhynchospora riedeliana</em></td>
<td>-</td>
<td>23.75 ± 0.17</td>
<td>26.00 ± 0.00</td>
<td>-</td>
<td>-</td>
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<tr>
<td><em>Lessingianthus linearifolius</em></td>
<td>5.99 ± 0.31&lt;sup&gt;a&lt;/sup&gt;</td>
<td>8.90 ± 0.64&lt;sup&gt;b&lt;/sup&gt;</td>
<td>8.15 ± 0.43&lt;sup&gt;c&lt;/sup&gt;</td>
<td>6.05 ± 0.16&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6.59 ± 0.14&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6.38 ± 0.43&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.20 ± 1.52&lt;sup&gt;a&lt;/sup&gt;</td>
<td>F=9.84 ***</td>
</tr>
<tr>
<td><em>Richterago arenaria</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Vellozia caruncularis</em></td>
<td>5.28 ± 0.38&lt;sup&gt;a&lt;/sup&gt;</td>
<td>9.75 ± 1.26&lt;sup&gt;b&lt;/sup&gt;</td>
<td>7.24 ± 0.43&lt;sup&gt;c&lt;/sup&gt;</td>
<td>5.11 ± 0.59&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.02 ± 0.69&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.45 ± 0.52&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4.05 ± 0.20&lt;sup&gt;d&lt;/sup&gt;</td>
<td>F=11.21 ***</td>
</tr>
<tr>
<td><em>Vellozia epidendroides</em></td>
<td>13.93 ± 0.68&lt;sup&gt;a&lt;/sup&gt;</td>
<td>23.87 ± 1.18&lt;sup&gt;b&lt;/sup&gt;</td>
<td>10.29 ± 0.71&lt;sup&gt;c&lt;/sup&gt;</td>
<td>13.26 ± 1.90&lt;sup&gt;a&lt;/sup&gt;</td>
<td>13.65 ± 0.38&lt;sup&gt;a&lt;/sup&gt;</td>
<td>10.33 ± 0.58&lt;sup&gt;c&lt;/sup&gt;</td>
<td>12.32 ± 0.79&lt;sup&gt;a&lt;/sup&gt;</td>
<td>F=20.30 ***</td>
</tr>
<tr>
<td><em>Vellozia resinosa</em></td>
<td>7.04 ± 0.40&lt;sup&gt;a&lt;/sup&gt;</td>
<td>21.02 ± 0.31&lt;sup&gt;b&lt;/sup&gt;</td>
<td>8.53 ± 0.55&lt;sup&gt;c&lt;/sup&gt;</td>
<td>7.96 ± 0.46&lt;sup&gt;c&lt;/sup&gt;</td>
<td>7.21 ± 0.30&lt;sup&gt;c&lt;/sup&gt;</td>
<td>7.91 ± 0.58&lt;sup&gt;c&lt;/sup&gt;</td>
<td>6.46 ± 0.12&lt;sup&gt;a&lt;/sup&gt;</td>
<td>F=93.86 ***</td>
</tr>
<tr>
<td><em>Vellozia variabilis</em></td>
<td>5.86 ± 0.38&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.94 ± 0.29&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6.86 ± 0.54&lt;sup&gt;c&lt;/sup&gt;</td>
<td>6.04 ± 0.59&lt;sup&gt;c&lt;/sup&gt;</td>
<td>5.27 ± 0.39&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.77 ± 0.29&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3.75 ± 0.26&lt;sup&gt;c&lt;/sup&gt;</td>
<td>F=13.30 ***</td>
</tr>
<tr>
<td><em>Xyris obtusiuscula</em></td>
<td>15.51 ± 0.29&lt;sup&gt;a&lt;/sup&gt;</td>
<td>15.17 ± 0.68&lt;sup&gt;a&lt;/sup&gt;</td>
<td>23.80 ± 1.45&lt;sup&gt;b&lt;/sup&gt;</td>
<td>13.00 ± 0.00&lt;sup&gt;a&lt;/sup&gt;</td>
<td>16.51 ± 1.91&lt;sup&gt;a&lt;/sup&gt;</td>
<td>15.10 ± 1.50&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-</td>
<td>F=8.40 ***</td>
</tr>
<tr>
<td><em>Xyris pilosa</em></td>
<td>10.24 ± 0.44&lt;sup&gt;a&lt;/sup&gt;</td>
<td>17.77 ± 1.06&lt;sup&gt;a&lt;/sup&gt;</td>
<td>14.89 ± 0.87&lt;sup&gt;c&lt;/sup&gt;</td>
<td>10.76 ± 0.69&lt;sup&gt;a&lt;/sup&gt;</td>
<td>8.10 ± 0.80&lt;sup&gt;d&lt;/sup&gt;</td>
<td>10.55 ± 0.77&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-</td>
<td>F=22.24 ***</td>
</tr>
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</table>
Table 3. Germination synchrony (mean ± standard error) of graminoid and forb species of *campos rupestres* grasslands. Low values indicate more synchronized germination and high values indicate asynchronous germination. Within a species, treatment values with different lower case letters were significantly different according to the GLM results.

<table>
<thead>
<tr>
<th>Species</th>
<th>Control</th>
<th>15°C/25°C</th>
<th>20°C/30°C</th>
<th>Charred wood</th>
<th>Water smoke</th>
<th>Dry heat</th>
<th>Soil</th>
<th>ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aristida torta</em></td>
<td>0.40 ± 0.18</td>
<td>0.21 ± 0.18</td>
<td>0.31 ± 0.18</td>
<td>0.34 ± 0.20</td>
<td>0.75 ± 0.28</td>
<td>0.00 ± 0.00</td>
<td>0.50 ± 0.32</td>
<td>F=0.71 NS</td>
</tr>
<tr>
<td><em>Lessingianthus linearifolius</em></td>
<td>0.87 ± 0.16&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>1.53 ± 0.14&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.23 ± 0.37&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.96 ± 0.17&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.82 ± 0.13&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>1.11 ± 0.21&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.26 ± 0.26&lt;sup&gt;b&lt;/sup&gt;</td>
<td>F=3.54 *</td>
</tr>
<tr>
<td><em>Vellozia caruncularis</em></td>
<td>1.56 ± 0.08</td>
<td>1.87 ± 0.07</td>
<td>1.90 ± 0.21</td>
<td>1.53 ± 0.07</td>
<td>1.50 ± 0.20</td>
<td>1.60 ± 0.11</td>
<td>1.58 ± 0.06</td>
<td>F=1.96 NS</td>
</tr>
<tr>
<td><em>Vellozia epidendroides</em></td>
<td>2.57 ± 0.03&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.64 ± 0.06&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.16 ± 0.06&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>1.10 ± 0.15&lt;sup&gt;d&lt;/sup&gt;</td>
<td>1.63 ± 0.06&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.24 ± 0.08&lt;sup&gt;ac&lt;/sup&gt;</td>
<td>1.90 ± 0.26&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>F=18.50 ***</td>
</tr>
<tr>
<td><em>Vellozia resinosa</em></td>
<td>1.92 ± 0.07&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.98 ± 0.10&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.78 ± 0.10&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.96 ± 0.12&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.79 ± 0.10&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.21 ± 0.12&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.45 ± 0.09&lt;sup&gt;b&lt;/sup&gt;</td>
<td>F=32.50 ***</td>
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<tr>
<td><em>Vellozia variabilis</em></td>
<td>1.55 ± 0.04</td>
<td>1.69 ± 0.07</td>
<td>1.88 ± 0.09</td>
<td>1.52 ± 0.17</td>
<td>1.42 ± 0.16</td>
<td>1.57 ± 0.07</td>
<td>1.54 ± 0.08</td>
<td>F=2.29 NS</td>
</tr>
<tr>
<td><em>Xyris obtusiula</em></td>
<td>1.53 ± 0.14&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.62 ± 0.22&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.82 ± 0.29&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.00 ± 0.00&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.37 ± 0.17&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.99 ± 0.33&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-</td>
<td>F=4.82 **</td>
</tr>
<tr>
<td><em>Xyris pilosa</em></td>
<td>2.22 ± 0.13&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.88 ± 0.19&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.14 ± 0.16&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.72 ± 0.10&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.13 ± 0.23&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.46 ± 0.06&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-</td>
<td>F=24.60 ***</td>
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</tbody>
</table>
Table 4. Viable, embryoless and dormant seeds (mean percentage ± standard error) for graminoid and forb species of *campos rupestres* grasslands. Dormant seeds were calculated as the final germination percentage over the total number of viable seeds.

ND: non-dormant seeds. NC: non-conclusive data. Embryoless seeds and viable seeds are in respect to total number of seeds.

<table>
<thead>
<tr>
<th>Species</th>
<th>Embryoless seeds (%)</th>
<th>Viable seeds (%)</th>
<th>Dormant seeds (%)</th>
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<tr>
<td><em>Aristida torta</em></td>
<td>55.00 ± 5.00</td>
<td>28.00 ± 3.79</td>
<td>67.9</td>
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<td><em>Echinolaena inflexa</em></td>
<td>13.52 ± 2.45</td>
<td>0.00 ± 0.00</td>
<td>NC</td>
</tr>
<tr>
<td><em>Lagenocarpus alboniger</em></td>
<td>54.00 ± 4.11</td>
<td>7.00 ± 1.37</td>
<td>NC</td>
</tr>
<tr>
<td><em>Lagenocarpus tenuifolius</em></td>
<td>14.50 ± 3.11</td>
<td>38.00 ± 3.47</td>
<td>100</td>
</tr>
<tr>
<td><em>Rhynchospora ciliolata</em></td>
<td>80.00 ± 2.50</td>
<td>5.00 ± 1.77</td>
<td>NC</td>
</tr>
<tr>
<td><em>Rhynchospora consanguinea</em></td>
<td>0.50 ± 0.56</td>
<td>39.50 ± 5.75</td>
<td>100</td>
</tr>
<tr>
<td><em>Rhynchospora riedeliana</em></td>
<td>37.00 ± 2.24</td>
<td>30.00 ± 4.68</td>
<td>100</td>
</tr>
<tr>
<td><em>Lessingianthus linearifolius</em></td>
<td>57.00 ± 1.37</td>
<td>41.00 ± 1.12</td>
<td>ND</td>
</tr>
<tr>
<td><em>Richterago arenaria</em></td>
<td>84.00 ± 4.47</td>
<td>1.00 ± 1.11</td>
<td>NC</td>
</tr>
<tr>
<td><em>Vellozia caruncularis</em></td>
<td>11.00 ± 5.70</td>
<td>86.00 ± 4.47</td>
<td>ND</td>
</tr>
<tr>
<td><em>Vellozia epidendroides</em></td>
<td>6.50 ± 2.27</td>
<td>89.50 ± 2.98</td>
<td>ND</td>
</tr>
<tr>
<td><em>Vellozia resinosa</em></td>
<td>3.00 ± 1.37</td>
<td>93.50 ± 2.44</td>
<td>ND</td>
</tr>
<tr>
<td><em>Vellozia variabilis</em></td>
<td>2.00 ± 2.23</td>
<td>89.00 ± 3.26</td>
<td>ND</td>
</tr>
<tr>
<td><em>Xyris obtusiuscula</em></td>
<td>3.00 ± 1.37</td>
<td>67.00 ± 2.85</td>
<td>56.7</td>
</tr>
<tr>
<td><em>Xyris pilosa</em></td>
<td>1.50 ± 0.68</td>
<td>89.50 ± 4.79</td>
<td>ND</td>
</tr>
</tbody>
</table>
**Fig. 1.** Germination percentage, mean germination time and synchrony of the fifteen *campo rupestre* species, southeastern Brazil. (a) Germination percentage (%), (b) Mean germination time (days) and (c) synchrony at 25°C, for post-fire fruiting and regularly fruiting Cyperaceae and Poaceae species. Different letters indicate significant differences according (a) GLM procedure (quasibinomial error distribution and logit
link function) with $F=28.08, P<0.001$, (b) GLM procedure (Gamma error distribution and inverse link function) with $F=33.46, P<0.001$, (c) simple ANOVAs, followed by post-hoc tests (Tukey's "Honest Significant Difference") $F=16.87, P<0.001$.)
Appendix:

Appendix 1: Pictures of the *campos rupestres* of Serra do Cipó: a) the mosaic of grasslands and rocky outcrops during the dry season, b) the mosaic of grasslands and rocky outcrops during the wet season.

Appendix 2: Plant list with family, plant form, distribution range and seed dispersal period.

Appendix 3: Life-history traits of the four species producing and dispersing seeds after a wildfire in August 2011.

Appendix 4: Average seed mass before and after soaking in tap water for 72h, with the increased seed mass percentage (%) for 15 herbaceous species from *campos rupestres* in Southeastern Brazil. Statistics refer to Wilcoxon tests.