Research Paper

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How does fire affect germination of grasses in the Cerrado?

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Abstract

Fire is a frequent disturbance in the Cerrado and is one of the major factors affecting vegetation structure and diversity. Fire events open gaps within the herbaceous layer and increase temperature fluctuation in the soil surface. In addition to being an important environmental filter for germination, fire is a germination cue for species with physiological dormancy. This study aimed to evaluate the germination of native grasses, using daily temperature fluctuations and heat shock to overcome physiological dormancy in native grasses. We also evaluated seed longevity after dispersal for some species. We conducted the daily temperature fluctuation experiments on seeds of ten native grass species, which were collected and then placed in germination chambers simulating thermal fluctuation throughout the day (19–55°C). We also subjected seeds to different heat-shock treatments: 100°C for 1 min, 100°C for 3 min and 200°C for 1 min. To determine seed longevity, we stored seeds for 6 and 12 months after collection and then set them to germinate (27°C, 12/12 h light). Non-germinated seeds from all experiments were tested for viability. Most species had low longevity and germination percentages. Those that had physiological dormancy were stimulated to germinate when exposed to temperature fluctuations. One species resisted temperatures up to 200°C. For all other species, neither treatment affected germination percentages. Our results indicate the importance of these environmental filters for seedling recruitment of these species, considering the low longevity and the presence of physiological dormancy.

Introduction

Tropical savannas are characterized by a continuous herbaceous layer, with C4 grasses being one of the most representative groups and the main fuel load for savanna fires (Trollope, 1982; Veldman et al., 2015). Fire is a common disturbance in these ecosystems (Bond and Van Wilgen, 1996) and plays an extremely important role in maintaining structure, diversity and vegetation physiognomy (Bond and Keeley, 2005). Furthermore, grasses vary greatly in morphological and physiological traits (Sarmiento, 1992) and are therefore highly resilient to fire (Bond, 2004).

Fire-prone species, including grasses, have protected buds and a storage reserve that allow some species to resprout immediately after a fire event ('resprouters'; Clarke et al., 2013; Pausas et al., 2018), and others to persist by seedling recruitment ('seeders'; Whelan, 1995; Bond and Van Wilgen, 1996). Grasses have different strategies that allow them to dominate in fire-prone ecosystems, being one of the most flammable components of the herbaceous layer (Simpson et al., 2016). For example, the C4 photosynthetic pathway facilitates the accumulation of biomass, inducing high photosynthetic rates and efficient use of nutrients (Osborne, 2008; Edwards, 2012). Moreover, grasses are the most resilient group to fire in tropical savannas, being able to resprout immediately after fire (Bond, 2004) since they allocate reserves (e.g. fructans) mostly to their roots (Moraes et al., 2013). Therefore, species from fire-prone ecosystems must have the ability to persist after fire events by resprouting or they have seed traits that respond to fire-related germination cues by resisting or promoting seedling emergence (Ramos et al., 2016; Zirondi et al., 2019).

Little is known about germination traits of grasses (but see Aires et al., 2014; Ramos et al., 2016). For some grass species, seedling recruitment is low despite high seed production (Foster, 2001; Foster and Tilman, 2003; Foster et al., 2007). Dormancy, environmental factors (such as water, light and fire), competition and longevity can affect the establishment of grass species by seeds (Cole et al., 2005; Commander et al., 2017). In tropical savannas, grasses usually produce a high proportion of empty diaspores (Carmona et al., 1998; Wright et al., 2014; Dayrell et al., 2016), and they generally have physiological dormancy (Baskin and Baskin, 2014; Dayrell et al., 2016; Erickson et al., 2016; Commander et al., 2017), which can be broken through exposure to high temperatures (see Ramos et al., 2016; Commander et al., 2017).

Table 1. Grass species sampled in the two sites (EEI: Estação Ecológica de Itirapina, Southeastern Brazil, an RNST: Reserva Natural Serra do Tombador, Central Brazil), in different vegetation types (CS: campo sujo, WG: wet grassland), with the date of collection and different treatments applied: TF – daily temperature fluctuation, HS – heath shock, and the species which had their longevity (L) tested

Species	Site	Vegetation type	Collection date	TF	HS	L
Andropogon lateralis L.	EEI	CS/WG	April 2016	x	x	x
Andropogon bicornis L.	EEI	CS/WG	April 2016	x	x	x
Aristida megapotamica Spreng.	EEI	CS	April 2016	x	x	x
Aristida riparia Trin.	EEI/RNST	CS	April 2016	x	x	x
Aristida jubata (Arechav.) Herter	EEI	CS	February 2016	x	x	
Axonopus aureus P. Beauv.	RNST	CS	October 2016	x		
Gymnopogon foliosus (Willd.) Nees	EEI	CS	June 2016	x	x	x
Loudetiopsis chrysothrix (Nees) Conert	EEI	CS/WG	April 2016	x	x	x
Sporobolus aeneus R.Br.	EEI	CS/WG	April 2016	x	x	x
Sporobolus cubensis Hitchc.	RNST	CS	October 2016	x	x	

Species from fire-prone ecosystems may have different strategies related to germination traits (Keeley et al., 2011; Lamont and He, 2017) that enable them to persist in the vegetation community. Seed dormancy and germination stimulation, for example, can be affected directly and indirectly by fire. During the fire, seeds will be exposed to heat shocks (Moreira et al., 2010) and smoke (direct effect – see Moreira et al., 2010; Stradic et al., 2015). Additionally, after the fire, seeds in the soil seed bank are exposed to daily temperature fluctuation as a result of the fire opening gaps in the vegetation (indirect effect – see Santana et al., 2013; Daibes et al., 2017). According to Ramos et al. (2016), grasses with dormant seeds tolerate exposure to high temperatures better than non-dormant seeds, with some species resisting 110°C for 5 min. Moreover, temperature fluctuation can break the dormancy of some grass species (Kolb et al., 2016).

Another important trait to evaluate is longevity and the capacity of seeds to resist high temperatures since most fires in the Cerrado occur during the dry season (Ramos-Neto and Pivello, 2000; Pivello, 2011) and most grass species disperse during the rainy season (Munhoz and Felfili, 2007; Ramos et al., 2014). Therefore, dormant seeds are assumed to be in the seed bank when the fire occurs. If seeds are still viable after the fire events, grass seedlings may be recruited when the first rains occur in the system. In general, native grass seeds have short longevity, reinforcing the formation of a transient soil seed bank for perennial species (Aires et al., 2014; de Andrade and Miranda, 2014), with many seeds losing their ability to germinate 1 year after dispersal (Thompson and Grime, 1979; Aires et al., 2014; Ramos et al., 2017).

To understand the mechanisms involved in the recruitment of native grasses of the Cerrado after the fire events, we aimed to understand the effects of fire on seed germination, conducting daily temperature fluctuation (indirect effect) and heat-shock (direct effect) treatments. Moreover, we analysed seed longevity of some grass species since longevity is a predictor of seed persistence in the soil (Thompson and Grime, 1979). The capacity to form a persistent soil seed bank implies a high potential among new individuals to establish in post-fire communities. We hypothesized that grass species from the Cerrado will have fire-resistant seeds, and that for dormant seeds, both the daily temperature fluctuation and heat-shock treatments would be sufficient to break physiological dormancy. Furthermore, we

expected grass seeds to have shorter longevity, which could be a limiting factor for seedling recruitment from the seed bank.

Materials and methods

Study area and seed collection

Seeds of native grasses were sampled in two different areas of the Cerrado: Estação Ecológica de Itirapina (EEI, Southeastern Brazil, 47°51′–47°48′ W and 22°11′–22° 15′ S, 2300 ha) and Reserva Natural Serra do Tombador (RNST, Central Brazil, 47°45′–47°51′ W and 13°35′–13°38′ S, 8900 ha). Both areas have a seasonal climate, with a well-marked dry season from May to September and a wet season from October to April. At the EEI, the average annual temperature is 22°C and the average annual precipitation is 1459 mm (Zanchetta et al., 2006). The RNST shows average temperatures ranging from 22 to 25°C and annual precipitation from 1300 to 1500 mm (Fundação Grupo Boticário, 2011). The main vegetation type at the seed collection site was *campo sujo* (Table 1), which is a vegetation dominated by a rich herbaceous layer with scattered shrubs and small trees (Coutinho, 1982). Two species were collected in both *campo sujo* (CS) and wet grasslands (WG; Table 1). The wet grasslands are dominated by a graminoid layer with Poaceae, Cyperaceae and Xyridaceae species, and the water table is closer to the soil surface (Cianciaruso and Batalha, 2008).

We collected seeds of ten native grass species in the two study areas (Table 1). Seeds were collected from different populations and individuals (>15 individuals) to guarantee genetic variability. They were sorted in the lab, and empty diaspores were counted (from a total of 100 seeds from each species; Table 2). Seeds were stored for no more than 3 months before germination trials, and only undamaged and full seeds were used. Seeds with less than 30% total germination were classified as having physiological dormancy (PD; Dayrell et al., 2016). We applied daily temperature fluctuation (TF) and heat-shock (HS) under dry conditions as our two treatments before putting seeds to germinate. We also tested seed longevity (see below for methods used). Furthermore, we tested seeds for longevity.

Daily temperature fluctuation experiments (TF)

To evaluate the effects of daily temperature fluctuation experienced by seeds dispersed after the fire, 4 replicates of 25 seeds

of each species were placed in germination chambers which simulated the temperature cycle throughout a single day (ranging from overnight lows of 19°C to peaks of 55°C with steps in temperature changes from low to high occurring every hour) for 45 days, and including a light regime of 12/12 h. Seeds were placed in Petri dishes with filter paper, but they were not watered, because we wanted to simulate the conditions experienced by seeds dispersed after fire before the rainy season since most of the fires in the Cerrado occur during the dry season. These temperatures were previously measured in the field for 90 days, and we used the average temperature of each hour of the day [for more information, see Daibes et al. (2017)]. Each replicate was placed in a different chamber to avoid pseudoreplication. Four replicates, with 25 seeds of each species, were not submitted to treatment (control) and were instead left for the same period, sequestered inside brown paper bags, under natural light conditions and room temperature oscillating between 24 and 26°C.

Heat-shock experiments (HS)

Only nine of the ten grass species were used for this experiment, due to the amount of available seeds (for more details, see Table 1). For each species, we submitted 5 replicates of 20 seeds to the following heat-shock treatments: 100°C for 1 min, 100°C for 3 min and 200°C for 1 min; and we had one control, which was not exposed to the heat shocks. We chose these temperatures following the studies of Miranda et al. (1993), which measured fire temperatures in different Cerrado vegetation types. Usually, fires in the Cerrado are fast, of low intensity and temperatures, consuming most of the aboveground biomass (Miranda et al., 1993; Rissi et al., 2017). Heat shocks were performed in a preheated electronic muffle, and each replicate was placed separately to avoid pseudoreplication.

Longevity

Seeds of seven grass species (Table 1) were stored in paper and ziplock bags at room temperature for 6 and 12 months after collection and were subsequently put to germinate. We used 4 replicates of 25 seeds for each species.

Germination procedures

After treatments (temperature fluctuation, heat shocks and longevity), seeds were placed in Petri dishes with two filter papers saturated with distilled water. These seeds were put to germinate in germination chambers (TECNAL – model TE-4013, germination chambers with photoperiod and ramp and level coordinator), with constant temperature (27°C), a light regime of 12/12 h (Fichino et al., 2016), and mean radiation activity of 82 lum. ft^{-2}. We performed observations three times a week for 30 days. Seeds that showed radicle or cotyledons were considered to be germinated and were removed from the Petri dishes. At the end of the germination trials, ungerminated seeds were submitted to the tetrazolium test (1%) to verify their viability (Lakon, 1949). These seeds were soaked in the tetrazolium solution in dark glass vials wrapped in aluminium foil and kept at 25–27°C for 24 h. Subsequently, the seeds were dissected, and those with tissue staining were considered viable seeds. For the species studied, 24 h under controlled conditions were ideal for staining of the embryo. The viability of the seeds that were not submitted to any type of treatments (control) was considered the initial

Table 2. Percentage of initial viable and empty seeds of native grasses of Cerrado

Species	Initial viability (%)	Empty seeds (%)	Dormancy type
Andropogon lateralis	84	11	ND
Andropogon bicornis	21	69	ND
Aristida megapotamica	35	40	ND
Aristida riparia	61	37	ND
Aristida jubata	56	31	ND
Axonopus aureus	79	28	PD
Gymnopogon foliosus	88	20	ND
Loudetiopsis chrysothrix	69	70	PD
Sporobolus aeneus	51	12	ND
Sporobolus cubensis	98	10	PD

Classification of species in non-dormant (ND) and dormant species (Physiological Dormancy – PD).

viability (Table 2). The percentage of germination was considered in relation to the total number of seeds used for each experiment, and the percentage of viability was related only to seeds with embryos. Finally, in species with high dormancy levels, viable embryos may not be detected by the tetrazolium tests (Ooi et al., 2004).

Data analyses

To analyse differences in germination and viability percentages for each treatment (TF, HS and L) and species, we used generalized linear models (GLMs) with a quasi-binomial error distribution (values in percentage of germinated seeds and their viability). *Post hoc* function in the Tukey's test was used to compare the effect of the TF, HS and L treatments with the control of each treatment. We analysed seed germination and seed viability separately, using the same model for both. For seed germination and seed viability, treatments (TF, HS and L) were used as a fixed effect. All analyses were performed using the R 3.2.5 software (R Development Core Team, 2016) with the packages vegan (Oksanen et al., 2019), *lme4* (Bates et al., 2015), *multcomp* (Hothorn et al., 2008), *lattice* (Sarkat, 2008) and *ggplot2* (Wickham, 2009).

Results

In general, species showed low percentages of empty diaspores, with only two species having no embryo in more than 50% of their seeds: *Andropogon bicornis* (69%) and *Loudetiopsis chrysothrix* (70%; Table 2). Moreover, two species had seed viability lower than 50%: *An. bicornis* (21%) and *Aristida megapotamica* (35%; Table 2). Among the study species, only three presented physiological dormancy: *Axonopus aureus*, *L. chrysothrix* and *Sporobolus cubensis* (Table 2).

Seed germination of most species was not affected by daily temperature fluctuations (Fig. 1; Supplementary Table S1). However, species with dormant seeds had higher germination percentages when this treatment was applied. *Ax. aureus* showed an increase in relation to the control (45%, $P = 0.01$; Fig. 1) as did *S. cubensis* (57%) and *L. chrysothrix* (25%) ($P = 0.006$ and $P = 0.001$,
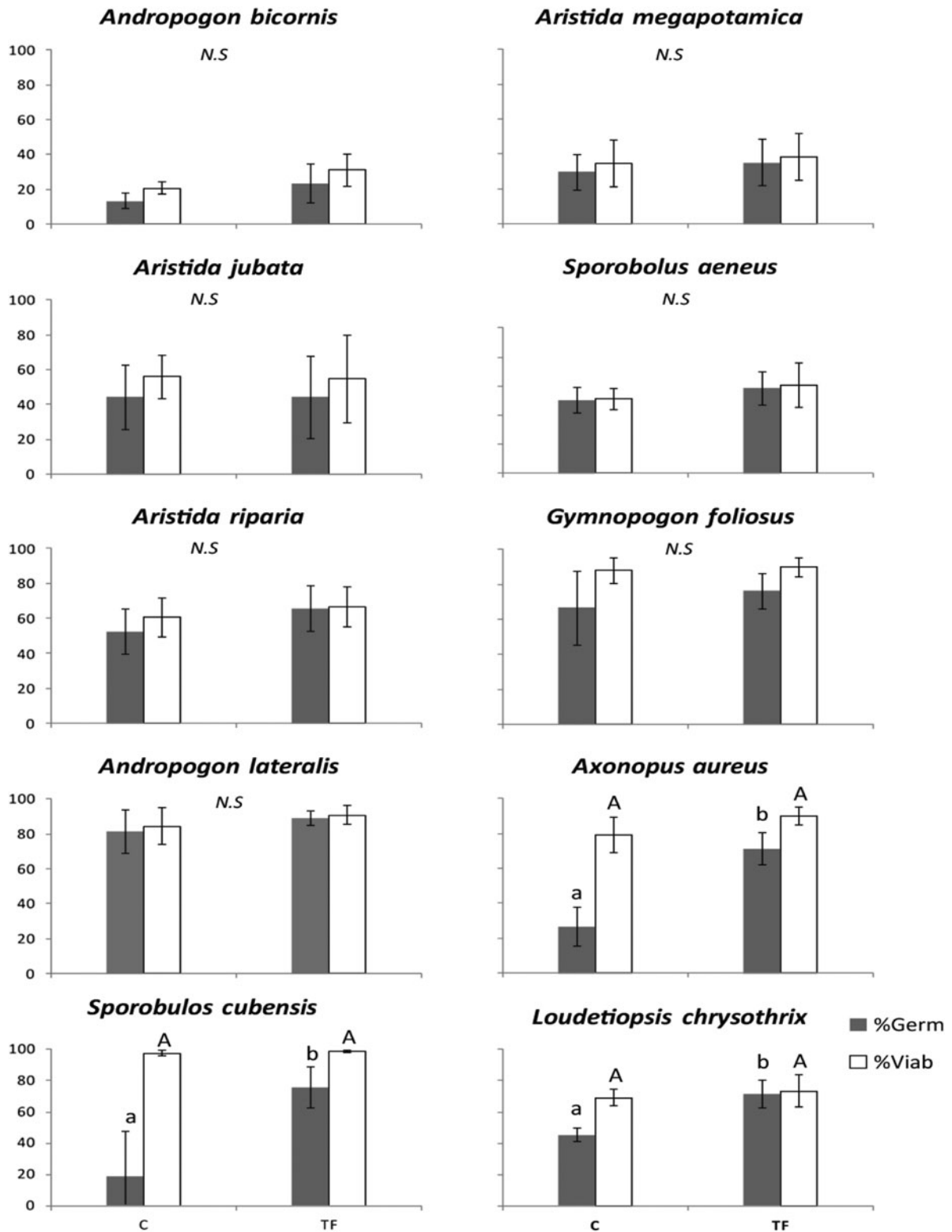
Fig. 1. Effects of daily temperature fluctuation on seeds germination (grey bar) and viability (white bar) of ten native grass species (mean ± SE) when exposed to the different treatments: C (control, no exposure to temperature fluctuation) and TF (temperature fluctuation). Different lowercase letters mean significant differences among treatments for seed germination and different capital letters mean significant differences among for seed viability ($P \leq 0.05$).

respectively; Fig. 1). The viability of all study species was not affected by temperature fluctuation (Fig. 1; $P > 0.05$).

Ar. megapotamica and *Gymnopogon foliosus* seeds resisted high temperatures, their germination and viability percentages

remaining unaffected by the tested temperatures (Fig. 2; $P > 0.05$). All species resisted up to 100°C for 1 min, neither germination nor viability being affected by the treatments (Fig. 2; $P > 0.05$). However, the exposure to 100°C for 3 min led to a 62% decrease
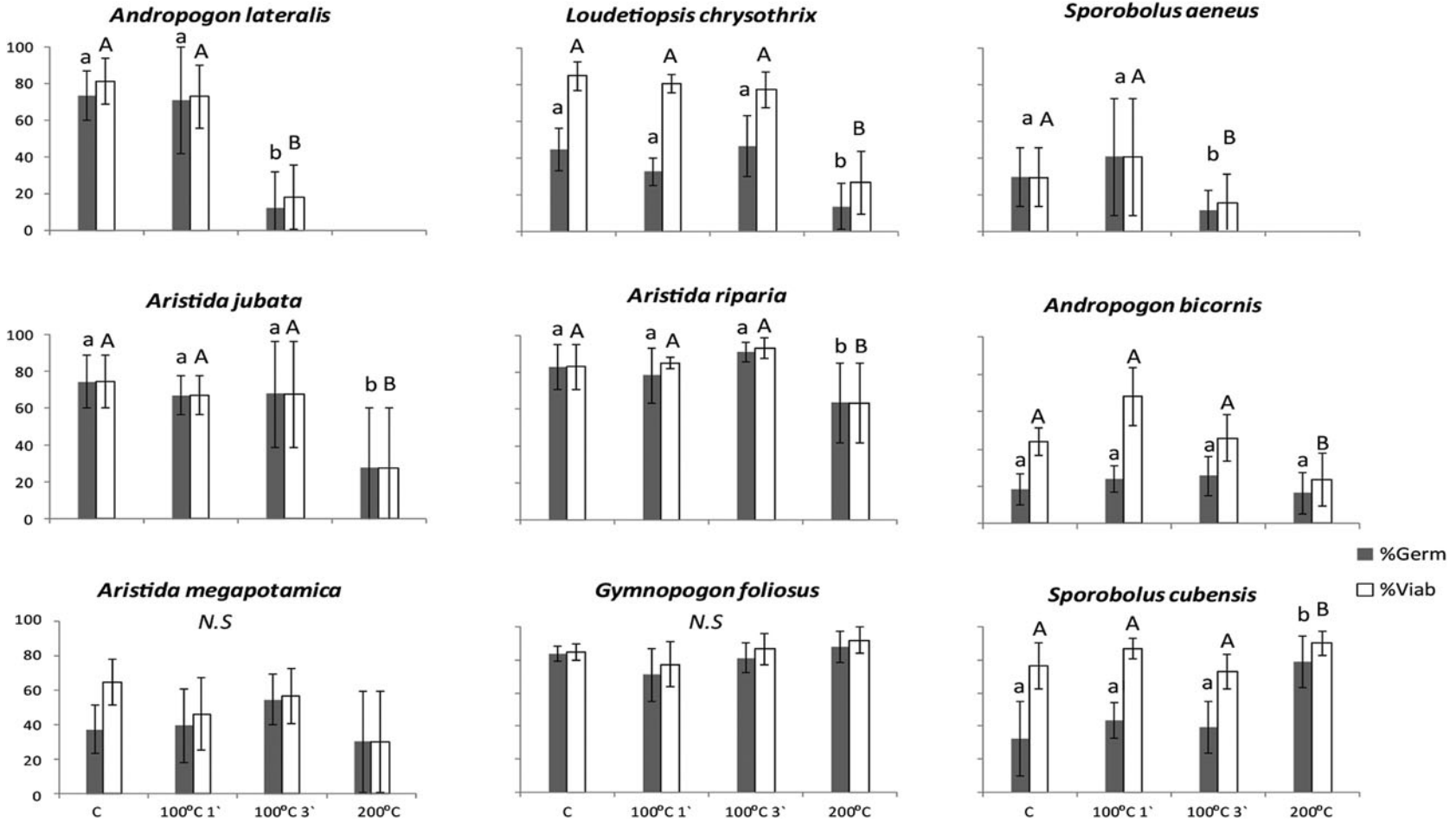
Fig. 2. Germination percentage (mean ± SE) of native grass species of Cerrado, according to the different heat-shock treatments: control (C), 100°C 1′, 100°C 3′ and 200°C 1′. Different letters mean significant differences among treatments for seed germination and different capital letters mean significant differences among for seed viability ($P \leq 0.05$).

Table 3. Germination and viability percentages (mean ± SD) for seeds from different native grass species of Cerrado just after seed collection (0) and 6 and 12 months after storage

Species	Germination (%)			Viability (%)		
	0	6	12	0	6	12
Andropogon bicornis	13 ± 4.41	7 ± 5.08	0	21 ± 3.6	13 ± 11.1	0
Andropogon lateralis	81 ± 12.54	72 ± 11	47 ± 17.7*	84 ± 10.5	76 ± 8.5	55 ± 15.8*
Aristida megapotamica	30 ± 10.05	84 ± 4.7**	95 ± 5**	35 ± 13.5	88 ± 3.5*	95 ± 5*
Aristida riparia	52 ± 10.6	10 ± 6.75*	28 ± 13.7*	61 ± 12.1	13 ± 7.7*	38 ± 18*
Gymnopogon foliosus	66 ± 21	85 ± 5.1	42 ± 17.1	88 ± 7.1	86 ± 6.2	53 ± 19.2
Loudetiopsis chrysothrix	45 ± 4.11	–	75 ± 10.32*	69 ± 5.2	–	80 ± 12*
Sporobolus aeneus	50 ± 8.7	47 ± 5.98	31 ± 13.21*	51 ± 7.2	47 ± 6	33 ± 12.4*

*$P \le 0.05$, **$P \le 0.001$.

in germination ($P = 0.004$; Fig. 2) and a 66% decrease in viability ($P = 0.005$; Fig. 2) of *Andropogon lateralis* seeds in comparison to the control. Seeds of *Sporobolus aeneus* also showed decreased germination and viability when exposed to 100°C for 3 min ($P = 0.02$ and $P = 0.05$, respectively; Fig. 2).

Most species showed a decrease in both germination and viability when exposed to 200°C. Two species did not germinate at all at this temperature, and all their seeds were dead after the treatment (*An. lateralis* and *S. aeneus*; Fig. 2). *L. chrysothrix*, *Aristida jubata* and *Aristida riparia* showed a significant decrease in germination and viability percentages (Fig. 2), while *An. bicornis* showed a 21% decrease in viability ($P < 0.001$); however, germination percentages among these species did not differ from the control when seeds were exposed to 200°C. Lastly, one species, *S. cubensis*, had its dormancy broken when seeds were exposed to 200°C and germination increased by 48% ($P = 0.006$; Fig. 2).

The germination and viability of seeds stored for 6 months were generally unaffected by time ($P > 0.05$; Table 3). However, *Ar. megapotamica* showed a 50% increase in germination and viability after 6 months ($P < 0.001$ and $P = 0.006$, respectively; Table 3). Conversely, seeds of *Ar. riparia* showed lower germination and viability percentages after 6 months ($P = 0.014$ and $P = 0.003$, respectively; Table 3).

After 1 year of storage, germination and viability of the seeds of *G. foliosus* were the same as at the beginning of the experiments ($P > 0.05$; Table 3). However, some species showed a significant decrease in both germination and viability, such as *An. lateralis* (34% in germination percentage and 29% in viability), *Ar. riparia* (24% in germination and 23% in viability) and *S. aeneus* (19% in germination and 18% in viability; Table 3). Seeds of *Ar. megapotamica* increased germination (66%, $P < 0.001$) and viability relative to the beginning of the experiments (60%, $P = 0.003$; Table 3), as did *L. chrysothrix* seeds, which showed higher germination and viability percentages after 1 year of storage ($P \le 0.05$; Table 3).

Discussion

Dormancy prevents germination of seeds of many different species in unpredictable environments where conditions favourable for recruitment are only brief. Germination of physiologically dormant (PD) seeds is directly influenced by environmental cues such as temperature, light or water availability (Baskin and Baskin, 2004) and is the most common type of dormancy in tropical savannas (Dayrell et al., 2016), particularly prevalent in grass

species (Carmona et al., 1998; Musso et al., 2014; Kolb et al., 2016). Understanding how these mechanisms interact with fire cues to promote seed germination is crucial to the understanding of post-fire plant regeneration in these ecosystems.

In fire-prone ecosystems, fire events are responsible for maintaining and influencing the structure and diversity of plant communities (Bond and Keeley, 2005), opening gaps within the vegetation (Fidelis et al., 2012), and creating new sites for species to establish (Grubb, 1977). Conditions in the gaps may differ from the rest of the system, with greater daily temperature fluctuation in the soil (Fidelis and Blanco, 2014; Santana et al., 2013; Daibes et al., 2017), which may directly influence seed recruitment. In this study, three species presented physiological dormancy: *Ax. aureus*, *L. chrysothrix* and *S. cubensis*. All three species had their dormancy broken by daily temperature fluctuation. In the Cerrado, gaps in vegetation cause differences in fire temperature on the surface, creating important safe-sites for seed germination and survival (Daibes et al., 2018). Thus, our study shows that temperature fluctuation is an essential mechanism for the germination of some grass species in Cerrado, confirming that fire heterogeneity is important for seedling regeneration.

On the other hand, daily temperature fluctuation did not affect germination and viability percentages of non-dormant species, indicating that their seeds tolerate a wide range of temperature in the soil. Some studies using Cerrado grasses showed that alternating two temperatures (e.g. 15/25°C or 20/30°C) affected seed viability negatively (Musso et al., 2014; Stradic et al., 2015). In contrast to the above-cited studies, which used only two temperature regimes and a single step each diurnal period, our study used temperature curves that simulated those measured in the field. This may influence the differences we found for non-dormant species. No effect on seed viability of non-dormant seeds, but also demonstrated that that daily temperature fluctuation affects positively seed germination of dormant seeds.

Fire itself influences seed germination by increasing temperatures during fire events, which could have positive (break of dormancy, see Keeley et al., 2011) and negative (kill seeds) effects on seed germination. We found one species, *Sporobolus cubensis*, whose dormancy was broken when exposed to 200°C, indicating not only that seeds of this species can survive fire but also that the high temperatures produced by fire enhance their germination. Native grass species resprout and flower rapidly after fire, releasing their seeds while gaps in the vegetation still exist (Fidelis et al., pers. comm.). Thus, the seedling establishment of

this species occurs through recruitment from the soil seed bank that accumulates after each fire event. This strategy is probably also used by other grass species with fire-related cues for germination in Cerrado areas, such as *Mesosetum ferrugineum* – this species' dormancy was broken after exposure to high temperatures (Ramos et al., 2016), and it resprouted and flowered vigorously after fire (Fidelis et al., pers. comm.). These seeds may present higher contents of heat-shock proteins (Wehmeyer et al., 1996), which could be an advantage in fire-prone ecosystems, being a response to fire events (adaptive traits; Keeley et al., 2011; Lamont and He, 2017) since 200°C can be reached only during fires.

In our study, all species with dormant and non-dormant seeds resisted temperatures up to 100°C for 1 min. Fire-prone species can be stimulated to germinate after fire, or they can be tolerant, their seeds' viability and capacity to germinate remaining unchanged (Paula and Pausas, 2008; Fichino et al., 2016). In open savannas, fire is usually fast, with low temperatures at the surface and even lower temperatures in the first 3 cm of the soil (Miranda et al., 1993; Rissi et al., 2017; Schmidt et al., 2017; Daibes et al., 2018). Therefore, seeds may be able to survive the passage of such fire in these savannas, as long as they are not directly damaged by the flames. A high percentage of survival among the seeds would ensure the maintenance of the soil seed bank, and it would enable seedling recruitment from the seed bank in post-fire environments.

However, seeds of the species *An. lateralis*, *L. chrysothrix* and *S. aeneus*, which were collected in both wet grasslands and in open savanna (*campo sujo*), showed lower fire resistance. This result suggests that the environmental conditions, in this case water availability, may also influence germination traits and responses to fire since the only two species that did not germinate and had viable seeds at 200°C were *An. lateralis* and *S. aeneus*. In Cerrado, fires in wet grasslands usually have a short residence time at 1 cm and a lower maximum temperature than fires in open savannas (Schmidt et al., 2017). Thus, the seeds of wet grassland species are usually not exposed to fires as hot as the ones in open savannas. Indeed, Ramos et al. (2016) also found that grass species from wet grasslands had lower germination percentages and lower resistance to fire temperatures than grass species of open savannas (*campo sujo*). These findings suggest that the evolution of fire-resistant seeds may be related to habitat moisture (Ramos et al., 2016).

Most of the studied grass species have seeds with low longevity, indicated by a gradual decline in viability percentages among the stored seeds, in comparison to freshly collected seeds. In some grass species, however, both germination and viability percentages increased after storage for 6 and 12 months. According to Martin (1946), grass seeds have fully developed embryos and, therefore, cannot present morphological dormancy. *Ar. megapotamica*, for example, showed a 25% increase in seed viability in this study. Thus, discarding the hypothesis of the occurrence of morphological dormancy, the increased germination and viability in these species could indicate that our tetrazolium tests were not sufficient to identify viable embryos in freshly sampled seeds of species with high dormancy levels, as observed in other fire-prone ecosystems (Ooi et al., 2004). These high levels of dormancy of this species might also have affected germination percentages (35%).

In summary, our study showed that the dormancy of Cerrado grass seeds was broken by exposure to daily temperature fluctuation and heat shock, two important fire-related germination cues in post-fire environments. In addition to the break of dormancy, most of the studied grass species had fire-tolerant seeds, confirming that resistance to fire is an important seed trait in Cerrado. These results reflect field conditions where dormant seeds are dispersed in the rainy season and remain in the soil for months before the onset of the next rainy season. The observed pattern can favour recolonization by grass species through seeds, which could be attributed to trade-offs between seed traits (resistance and break of dormancy) and environmental factors (high temperatures and temperature fluctuation). However, the longevity of these seeds suggests the formation of a transitory seed bank during a limited period per year, indicating a limiting factor in the success of native grass species' regeneration from the seed bank.

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