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Fire cues and germination of invasive and native grasses in the Cerrado

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ABSTRACT

Fire-related cues may enhance seed recruitment in flammable ecosystems and differences in fire-germination responses of invasive vs. native species can drive the invasion process. We evaluated the effects of heat shock and smoke water solution treatment on seed germination of invasive (*Melinis minutiflora*, *Urochloa decumbens*, *U. brizantha*) and native grasses (*Axonopus pressus*, *Aristida setifolia*, *Gymnopogon foliosus*) of the Cerrado. The effect of fire temperature was tested by exposing seeds to heat shock treatments of 60, 100, and 200 °C for one minute, comparing them to untreated seeds. The effect of smoke was tested by soaking seeds for 24-h in an aqueous smoke comparing them to seeds soaked in distilled water. Differences among treatments were evaluated by ANOVA and randomization tests. None of the tested species had germination stimulated by the temperature or smoke. Both species of *Urochloa* experienced decreased viability with increasing temperature, while seeds of native species and *M. minutiflora* tolerated heat shock up to 200 °C. The invasive grasses usually germinated faster than the native grasses. Germination time is therefore a crucial trait driving the invasion process, irrespective of fire-related cues. Other seed traits (*e.g.* dormancy) and higher resprouting capacity may help invasive species to persist in frequently burned savannas.

Keywords: African grasses, Cerrado grasses, fire temperature, *Melinis minutiflora*, smoke solution, *Urochloa brizantha*, *Urochloa decumbens*

Introduction

Successful germination and seedling establishment are important regeneration traits that lead to effective processes of biological invasion (Pyšek & Richardson 2007; Gioria & Pyšek 2017). In disturbed ecosystems, potentially invasive species are often more adapted to disturbance regimes when compared to the native ones (Facon *et al.* 2006). Fire is a principal disturbance in many ecosystems, and its effects depend on its origin (natural, by a lightning strike, or accidental, by human actions), season and intensity (Whelan 1995), as well as on the particular adaptations of the community species (Huston 2004; Lockwood *et al.* 2007).

At a community level, fire could affect plants by altering species richness, composition and structure (Whelan 1995; Fidelis *et al.* 2012). At the individual level, some species (such as grasses) could have a rapid regrowth, increased productivity, flowering and seed production after fire (Whelan 1995). Fire also could affect the survival, viability and germination of seeds (Moreira *et al.* 2010; Clarke & French 2005).

Seed exposure to fire-related germination cues may enhance recruitment of both invasive and native species (Adkins & Peters 2001; Figueroa *et al.* 2009; Arán *et al.* 2013). Heat shock and plant-derived smoke solutions, for instance, can stimulate germination of many grass species in fire-prone ecosystems (Clarke & French 2005). On the

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other hand, little effect of heat shock and exposure to smoke solution in germination has been reported for herbaceous species from Brazilian grasslands and savannas (Overbeck *et al*. 2006; Stradic *et al*. 2015; Fichino *et al*. 2016; Ramos *et al*. 2016; Paredes *et al*. 2018).

However, seeds of many Cerrado (Ribeiro *et al*. 2013; Fichino *et al*. 2016) and Chaco species (Jaureguiberry & Díaz 2015) may tolerate exposure to temperatures up to 100 °C. Therefore, seed survival to fire has been suggested as a critical trait for post-fire regeneration (Pausas *et al*. 2004; Paula & Pausas 2008; Ramos *et al*. 2016). Species that have fire-tolerant seeds and are able to promptly germinate after fire may have a competitive advantage in post-fire environments (Ramula *et al*. 2015). Hence, in Brazil, seed tolerance to high temperatures, rather than fire-stimulated germination, appears to promote species' survival in fire-prone environments (Fichino *et al*. 2016; Fidelis *et al*. 2016) and may foster biological invasion after fire events (Paredes *et al*. 2018).

Fire has been present in the Cerrado for millions of years, and has received some academic and scientific attention (Simon *et al*. 2009). Nevertheless, few studies have investigated the direct effects of fire on germination of Cerrado grass species (but see Ramos *et al*. 2016; Paredes *et al*. 2018). In addition to the native species, C_4 African grasses (such as *Urochloa* spp., previously *Brachiaria*) were introduced in Brazil for cattle forage (Pivello *et al*. 1999a; b; Durigan *et al*. 2007; Ziller & Dechoum 2013). Such African grasses have spread from the pastures and became a threaten to Cerrado native herbs by reducing their biomass and diversity (Pivello *et al*. 1999a; b; Damasceno *et al*. 2018).

Invasive grasses can also change fire behaviour by enhancing flame height and temperature, thus increasing the mortality of native species (Mistry & Berardi 2005; Gorgone-Barbosa *et al*. 2015). Improved understanding of the direct effects of fire on seed germination and on seedling recruitment may provide useful insight to control these species in protected areas (Paredes *et al*. 2018). Therefore, understanding fire effects at early stages of plant development is fundamental to elucidating biological invasion processes (Pyšek & Richardson 2007). Studies of post-fire regeneration strategies of invasive and native species are also crucial for planning of conservation and management programs (Paredes *et al*. 2018). Such programs may include prescribed fire management in order to identify mechanisms of post-fire competitive advantage of the invasives, and thus avoid their proliferation in burned areas.

Because Cerrado is subjected to frequent fires, we initially expected seeds of native and invasive grasses to respond to fire-related cues (high temperature and smoke water solution, a proxy for smoke) by tolerating or benefitting from fire. Given that several African grasses outcompete Cerrado grasses and become invasive (Pivello *et al*. 1999a; b) we hypothesized higher seed survival/germination of such African grasses under fire events compared to native Cerrado grasses. Therefore, in this study we aimed to evaluate the effects of heat shock and smoke (fire-related cues) on seed viability, germination percentage, and mean germination time (MGT) of three invasive (*Melinis minutiflora*, *Urochloa decumbens* and *Urochloa brizantha*), and three native (*Axonopus pressus*, *Aristida setifolia* and *Gymnopogon foliosus*) grass species frequently found in open Cerrado. Specifically, we assessed (1) the effect of heat shock (60, 100 and 200 °C) and (2) the effect of smoke water solution on seed germination.

Materials and methods

Focal species

We tested germination of six grasses that commonly co-occur in the Cerrado: three native species: *Axonopus pressus* (Nees ex Steud.) Parodi, *Aristida setifolia* Kunth and *Gymnopogon foliosus* (Willd.) Nees, and three of the most aggressive invasives: *Melinis minutiflora* P. Beauv, *Urochloa decumbens* (Stapf) R.D. Webster and *Urochloa brizantha* (Stapf) Webster (Pivello *et al*. 1999a; b). *Urochloa* species are perennial grasses that copiously resprout after fire, but their seeds might also germinate under temperatures up to 50 °C (Gorgone-Barbosa *et al*. 2016). *Melinis minutiflora*, although able to resprout, apparently regenerates primarily through seeds (Lorenzi 2008). Among the native species, *A. pressus* and *A. setifolia* can resprout after fire, while *G. foliosus* is an annual grass. Germination percentages of *A. setifolia* and *G. foliosus* are usually higher than 50 % (Carmona *et al*. 1998; 1999; Kolb *et al*. 2016), while *A. pressus* shows a high proportion of empty seeds (E Gorgone-Barbosa unpubl. res.), and thus low germination percentage (Kolb *et al*. 2016).

Seed collection

Since the three invasive species are widely commercialized, we used commercial seeds obtained from certified producers. The selected native species were collected in patches of *campo sujo*, which is an open Cerrado physiognomy dominated by grasses and forbs with scattered shrubs and dwarf trees (Coutinho 1978). *Axonopus pressus* and *G. foliosus* were collected in Itirapina Ecological Station (22°15'S 47°49'W; Southeastern Brazil), and *A. setifolia* was collected in a private property (close to the Jalapão State Park) in the Tocantins state (10°22'S 46°40'W; Northern Brazil).

Seeds of each species were collected from at least 20 individuals and stored at room temperature for less than three months until the beginning of the experiments. Heat shock experiments were conducted first, and smoke solution effects tested with a difference of around two months later. Prior to the experiments, the seeds were visually screened to avoid malformed and/or empty seeds, which were discarded. Detachable parts of the propagules (usually the glumes and palea) were also carefully removed, avoiding any mechanical damage to the seed.

Germination experiments

To test seed responses to fire cues, we subjected them to heat shocks and smoke solutions, under laboratory conditions. We subjected seeds to dry heat shocks of 60 °C, 100 °C and 200 °C for one minute in a pre-heated electric oven. These treatments were chosen based on field-recorded fire temperatures (Coutinho 1978; Miranda *et al*. 1993; Daibes *et al*. 2018). Belowground temperatures reach up to 60 °C in the soil seed bank and increase with aboveground fuel load (Daibes *et al*. 2017). When exposed at the soil surface, seeds face temperatures >100 °C, mostly being killed by temperatures >200 °C (Daibes *et al*. 2018). Moreover, Cerrado fires are fast and rapidly consume the herbaceous biomass, therefore the heat pulse rarely reaches more than a few minutes (Miranda *et al*. 1993; 2002).

For the heat shock treatments, we used five replicates of 20 seeds per treatment for each of the six species. We placed each replicate separately into the oven to avoid pseudo-replication (Morrison & Morris 2000). Seeds of the different study species were exposed to the treatments all together at the same time, but separately for each replicate. Control seeds were not exposed to heat shock (untreated seeds).

We used smoke water as a proxy for smoke to examine smoke effects. We prepared aqueous smoke solutions following the methodology adapted by Moreira *et al*. (2010) and Fichino *et al*. (2016). We heated 5 g of dry aboveground biomass — composed mostly of native grasses from an open Cerrado savanna — in an oven for 30 min at 200 °C. Immediately after removing the biomass from the oven, we added 50 ml of distilled water into the material and, after 10 minutes, we filtered the solution in filter paper (Whatman n°1). We prepared one solution for each replicate to avoid pseudo-replication. Subsequently, seeds were soaked in the aqueous smoke solution for 24 hours. Control seeds were soaked in distilled water for the same period.

After both experiments, seeds were placed in Petri dishes (60 mm diameter) with moistened filter paper (distilled water) and placed in germination chambers at a constant temperature of 27 ºC and light cycle of 12 h (according to Fichino *et al*. 2016). Seeds were observed every two days for 30 days. We counted and removed germinated seeds that showed primary root protrusion (Bewley *et al*. 2013). By the end of germination experiments, we tested non-germinated seeds of the control and heat shock experiments for viability, using a 1 % tetrazolium salt solution (pH 7) (Hilhorst 2011).

Data analysis

We calculated the percentage of germination and the mean germination time (MGT), according to Ranal & Santana (2006). Besides germination, seed survival could also be affected in the heat shock treatments, and therefore we calculated the total seed viability as the germination percentage + the seeds stained as viable by the tetrazolium tests. Separately for each species, we performed one-way analysis of variance (ANOVA) with permutation tests (10,000 iterations, Euclidean distance between sampling units) to verify the effect of treatments (heat shocks and smoke solution) on seed viability, germination percentage, and MGT. Because germination times are crucial to determine the early steps of invasion process (Gioria & Pyšek 2017; Gioria *et al*. 2018), we also verified differences in the MGT among species, independently of the treatment. In all analyses, we used permutation tests since there are no assumptions regarding normal data distribution. All statistical analyses were performed using the software MULTIV (Pillar 2006).

Results

The invasive *M. minutiflora* showed germination percentages around 60 %, regardless of the heat shock treatment (Tab. 1), and average MGT of 5.1 days (Tab. 2). Additionally, *M. minutiflora* seed viability was not affected by any of the heat shocks (Tab. 3). Seed germination of *U. decumbens* varied from 25 to 42 %, but showed no significant difference among temperatures (Tab. 1), while MGT was < 4.3 days in all heat shock treatments (Tab. 2). Seed viability of *U. decumbens* was significantly reduced at 100 and 200 °C (Tab. 3). Seeds of *U. brizantha* showed germination percentages around 60 %, but it was reduced to <20 % when seeds were subjected to 200 °C (Tab. 1). Average MGT was of 4.7 days and it was not affected by heat shock treatments (Tab. 2). Viability of *U. brizantha* also showed values ca. 15 % higher than seed germination in the control and showed an abrupt reduction in the hottest treatment (Tab. 3).

Heat shock did not affect germination of native grasses. *Aristida setifolia* seeds showed high germination percentages (from 63 to 75 %) and viability higher than 70 %, both not affected by any of the temperatures (Tabs. 1 and 3 respectively). MGT of *A. setifolia* varied from six to nine days, with no difference among treatments (Tab. 2). On the other hand, low germination percentages and viability (≤ 20 %, Tabs. 1, 3) were observed in *A. pressus* in all treatments, showing a slow MGT (14.3 days on average, Tab. 2). *Gymonopogon foliosus* had germination percentages always higher than 60 % and seed viability of nearly 100 % in all treatments (Tabs. 1 and 3, respectively). In contrast to the other two native species, *G. foliosus* seeds germinated very fast – on average 2.5 days – with no difference among treatments (Tab. 2).

Neither germination percentage nor MGT of invasive and native species were affected by the smoke solution treatment. Despite the variation, values were not statistically different (Tab. 4). Native species germination percentages were ca. 60 % for *G. foliosus* and *A. setifolia* (from 54 to 64 %) and lower for *A. pressus* (from 26 to 32 %) when subjected to smoke solution, indicating no treatment effect (Tab. 4).

Table 1. Germination (%, mean ± SE) of invasive species (*Melinis minutiflora*, *Urochloa brizantha* and *Urochloa decumbens*) and native species (*Aristida setifolia*, *Axonopus pressus* and *Gymnopogon foliosus*) seeds submitted to dry heat shocks of one minute at 60 °C, 100 °C and 200 °C, and the control (not exposed to high temperatures). Different letters mean significant differences among treatments of (*P* ≤ 0.05) according to one-way ANOVA with permutation tests.

Species	Control	60 °C	100 °C	200 °C	P
Invasives					
Melinis minutiflora	66±10	56±9	64±	60±10	0.44
Urochloa decumbens	42±13	35±12	25±9	25±12	0.39
Urochloa brizantha	58±6a	58±16a	58±15a	17±10b	0.0005
Natives					
Aristida setifolia	67±14	74±6	63±20	77±15	0.30
Axonopus pressus	12±3	11±8	7±7	17±10	0.21
Gymnopogon foliolosus	75±10	62±12	69±15	66±14	0.44

Table 2. Mean germination time (MGT, days, mean ± SE) of invasive and native species seeds submitted to dry heat shock treatments of one minute at 60 °C, 100 °C and 200 °C, and the control (not exposed to high temperatures). *P* values of temperature comparisons (*P* ≤ 0.05) according to one-way ANOVA with permutation tests.

Species	Control	60 °C	100 °C	200 °C	P
Invasives					
Melinis minutiflora	5.4±1.0	4.7±0.5	4.9±0.9	5.4±1.3	0.46
Urochloa decumbens	4.3±0.8	3.5±0.3	4.1±0.8	4.3±0.3	0.11
Urochloa brizantha	4.5±0.8	4.7±0.9	4.9±1.3	4.9±0.6	0.24
Natives					
Aristida setifolia	9.0±1.2	8.3±0.6	7.5±2.7	6.3±0.9	0.39
Axonopus pressus	15.4±6.4	12.9±7.2	15.2±5.8	13.7±3.4	0.22
Gymnopogon foliosus	2.3±0.1	2.3±0.2	2.4±0.2	2.9±0.6	0.48

Table 3. Viability (%, mean ± SE) of invasive species (*Melinis minutiflora*, *Urochloa brizantha* and *Urochloa decumbens*) and native species (*Aristida setifolia*, *Axonopus pressus* and *Gymnopogon foliosus*) seeds submitted to dry heat shocks of one minute at 60 °C, 100 °C and 200 °C, and the control (not exposed to high temperatures). Different letters mean significant differences among treatments (*P* ≤ 0.05) according to one-way ANOVA with permutation tests.

Species	Control	60 °C	100 °C	200 °C	P
Invasives					
Melinis minutiflora	67±12	58±9	64±	60±10	0.52
Urochloa decumbens	59±14a	50±15a	32±13b	37±18b	0.02
Urochloa brizantha	74±11a	68±13a	63±12a	34±13b	<0.0001
Natives					
Aristida setifolia	18±12	78±9	74±11	82±13	0.40
Axonopus pressus	21±6ab	14±9ab	10±8a	26±9b	0.03
Gymnopogon foliolosus	100	100	100	97±5	0.27

Table 4. Germination percentage and mean germination time (MGT, days, mean ± SE) of invasive and native species submitted to aqueous smoke solutions and the control (distilled water); *P* values of germination and temperature comparisons (*P*≤0.05) according to one-way ANOVA with permutation tests.

	Germination (%)			MGT		
Species	Control	Smoke	P	Control	Smoke	P
Invasives						
Melinis minutiflora	87±7	81±5	0.51	5.7±0.6	5.7±1.3	0.36
Urochloa decumbens	79±6	74±11	0.33	4.5±0.4	4.0±0.8	0.94
Urochloa brizantha	43±7	62±12	0.32	5.8±1.1	4.3±0.7	0.22
Natives						
Aristida setifolia	54±10	64±6	0.51	14.3±1.3	13.8±3.2	0.46
Axonopus pressus	26±3	32±6	0.56	6.3±1.5	6.8±1.2	0.39
Gymnopogon foliosus	64±6	58±9	0.58	3.5±2.8	2.1±0.1	0.58

When comparing MGT among the six species independently of treatment (combining heat shock and smoke), we observed that seeds of invasive species germinate approximately twice as fast as the native ones (*P* <0.0001), except for the native *G. foliosus*, which had the lowest MGT value (2.5 days, *P* <0.001 – Tab. 5).

Table 5. Mean germination time (days, mean ± SE) of invasive and native species seeds independently of the treatment. Different letters mean significant differences among species (*P* ≤ 0.05) according to one-way ANOVA with permutation tests.

Species	MGT
Invasives	
Melinis minutiflora	5.1±0.9a
Urochloa decumbens	4.0±0.5ab
Urochloa brizantha	4.7±0.9ab
Natives	
Aristida setifolia	8.2±0.8c
Axonopus pressus	14.3±5.7d
Gymnopogon foliolosus	2.4±0.2b

Discussion

Fire cues did not trigger germination of the study species, regardless of whether they were invasive or native grasses. On the contrary, heat shock decreased germination and/or viability of the invasive *Urochloa* spp. Such results contrast with other invasive species elsewhere (Arán *et al.* 2013; Cóbar-Carranza *et al.* 2015), and therefore fire-related cues apparently do not directly facilitate the invasion of these African grasses in the Cerrado savannas. Seeds of the invasive *Melinis minutiflora* and the native species were not affected by high temperatures, corroborating similar results described for native and invasive grasses in the Cerrado, under temperatures from 50 to 150°C (Paredes *et al.* 2018).

Because seeds of the native grasses retained their viability similar to controls under the hottest treatment (200 °C), their tolerance to high temperatures can be considered as an important trait for persisting under Cerrado fires (Ramos *et al.* 2016). Hence, fire survival may provide propagule supply for the species regeneration in frequently burned environments (Overbeck *et al.* 2006; Fichino *et al.* 2016). However, fire temperatures just below the soil surface increase only a few degrees during Cerrado typical fires (Miranda *et al.* 1993; Daibes *et al.* 2017). Therefore, most propagules of either invasive or native species would survive during fires when incorporated to the soil seed banks.

Persistence of buried propagules in the soil seed banks would thus allow the recolonization of the recently burned environment. Hence, recruitment from seed occurs with the onset of the well-marked rainy season in Cerrado (Andrade & Miranda 2014; Ramos *et al.* 2017). Once seeds survived fire heat shock, indirect effects of disturbance could thus benefit their germination in the post-fire environment. Such effects include enhanced temperature fluctuations, which may break physiological dormancy of invasive grasses (Musso *et al.* 2015; Gorgone-Barbosa *et al.* 2016). Other factors related to biomass removal could be related to reduced competition and/or favourable microsites, but competitive interactions between invasive and native species are still poorly understood and difficult to measure in the field (Zouhar *et al.* 2008).

Our results showed no effect of smoke water on germination, similar to the lack of smoke-mediated germination which has been reported for Cerrado species in the literature (Stradic *et al.* 2015; Fichino *et al.* 2016). This absence of a positive response strongly contrasts to germination of Australian grasses, which show smoke-stimulated germination (Clarke & French 2005). However, smoke has recently been suggested to enhance root growth of Cerrado seedlings (Ramos *et al.* 2019). Moreover, the effect of smoke solution depends on concentration and environmental interactions, as reported for Mediterranean ecosystems (Crosti *et al.* 2006; Moreira & Pausas 2018). Because germination of grasses can be light-dependent (Carmona *et al.* 1998; Baskin & Baskin, 1998), further studies should also consider the role of smoke on stimulating germination under dark conditions (see Gardner *et al.* 2001). Such an approach could help to explain the post-fire germination of propagules buried in soil seed banks.

Irrespective of fire-related cues, a shorter germination time has been demonstrated to enhance species' invasiveness (Pyšek & Richardson 2007; Gioria & Pyšek 2017). In accordance with that, our results showed that MGT was usually lower for the invasive species compared to the native ones. In disturbed environments, seeds shall at first place survive fires and then find conditions for germination to occur, thus the timing of germination is actually one aspect of a more complex process. Therefore, invasive species could show a competitive advantage for quickly recolonizing the post-fire environment (Jauni *et al.* 2015; Gioria *et al.* 2018). The exception was *G. foliosus*, a native species that showed the lowest MGT of all studied species. Being an annual species, its population persistence after fire relies only on regeneration from seeds (Pausas & Keeley 2014) and, therefore, germination time becomes critical for this species' survival.

Hence, germination of both *M. minutiflora* and *G. foliosus* may be favoured in the post-fire environment, given their seed tolerance to high temperatures and rapid germination. However, several other regeneration traits, such as high seed production, have been recognized to increase invasiveness (Pyšek & Richardson 2007). *Melinis minutiflora* produces more than 70,000 seeds/m^2 (Martins *et al.* 2009) with high viability and persistence in the soil seed bank — for more than three years (Carmona & Martins 2010). These traits may promote a rapid post-fire establishment, increase competitiveness over the natives and facilitate the invasion (Lake & Leishman 2004; Tierney & Cushman 2006).

Resprouting ability is also a post-fire regeneration strategy (Pausas *et al.* 2004). Therefore, many species from fire-prone environments may persist by forming a bud bank (Fidelis *et al.* 2014), rather than post-fire recruitment from the seeds (Paula & Pausas 2008). This could be the case of *Urochloa* spp., considering that — despite the reduced germination and viability percentages under the highest temperatures — *U. brizantha* has shown a remarkable capacity for post-fire resprouting (Gorgone-Barbosa 2016). Hence, once seeds have colonized (and established in) a certain area, resprouting seems to be a major strategy to warrant *Urochloa* persistence after fire. This ability is so effective that may provide advantage to *Urochloa* species even over *M. minutiflora* in the invaded habitats where they co-occur (Pivello *et al.* 1999a).

In summary, seeds of native grasses are tolerant to Cerrado fires, as well as seeds of the invasive *M. minutiflora*. On the other hand, *U. brizantha* and *U. decumbens* seeds are sensitive to hotter temperatures (100 and 200 °C) and rely mostly on resprouting to persist in the burned savannas, although a proportion of seeds would probably tolerate fire temperatures if incorporated into the soil seed bank. In general, invasive species showed the ability to germinate faster than most natives, which helps to explain their invasiveness in the Cerrado. Smoke solution showed no effect either on invasive or native species, but further research is needed to explore this topic. The information obtained in this research is fundamental to elucidate post-fire invasion process in the Cerrado and may guide management strategies for controlling invasive species.

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