



Fire-simulating temperatures do not affect seed imbibition and germination of *Vochysia tucanorum* Mart., a woody species from the Cerrado

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Abstract The colonization of new spaces in post-fire environments depends on habitat availability and the capacity of these environments to provide suitable microclimatic conditions for germination. Furthermore, the persistence of non-dormant woody species in fire-prone environments is influenced by the effects of fire passage on their seed germination. Thus, we investigated the effects of heat shocks on the imbibition and germination of *Vochysia tucanorum* Mart. (Vochysiaceae) seeds under temperature fluctuations simulating post-fire conditions in the cerrado *sensu stricto*. The seeds tolerated the applied heat shock without compromising the evaluated parameters, indicating that 70 °C for 5 min neither affected seed imbibition nor seed germination under temperature fluctuations. This ensures seed survival and germination in post-fire environments. Thus, this study provides new insights to evaluate persistence in other non-dormant species in post-fire environments.

Keywords Fire · Heat shock · Non-dormant seeds · Savanna · Woody species

1 Introduction

Savannas are fire-prone environments due to the accumulation of grasses that emerge during the rainy season and subsequently dry out, providing fuel for fire ignition and its spread during the dry season (Higgins et al. 2000; Newberry et al. 2020). One of the primary effects of fire is the increase of soil and air temperatures, leading to biomass combustion and alterations in vegetation structure and composition (Napier & Chipman, 2021). As a recurrent disturbance, fire also acts as an environmental filter, selecting species with traits that enable them to withstand high temperatures (Simon et al. 2009).

Following fire events, environmental conditions are substantially altered, particularly at the microclimatic level. Post-fire environments often exhibit greater temperature fluctuations, with higher daytime and lower nighttime temperatures compared to pre-fire conditions (Bradstock & Auld, 1995; Daibes et al. 2017). While vegetative resprouting is a common persistence strategy (Dantas & Pausas 2013; Pausas et al. 2018; Pilon et al. 2020), successful recruitment also depends on seed survival and establishment under these harsh and dynamic conditions.

In addition to vegetative persistence, fire strongly influences plant reproductive processes, particularly those involving seeds. Fire can trigger responses such as flowering (see also Zironi et al. 2021), fruit opening, and seed release, as well as stimulate germination from soil seed banks (Lamont et al. 2018). Moreover,

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seed dispersal from unburned to burned areas allows species to colonize newly available niches created by fire (Coutinho 1977; Nolan et al. 2021). Post-fire environments are also characterized by increased light availability and altered temperature and moisture conditions, which directly affect seed germination and recruitment (Macedo & Rossatto 2026).

These dynamics are evident in the vegetation of the Cerrado, also known as the Brazilian savanna, which comprises a mosaic of phytophysiognomies ranging from open fields to closed woodlands (Coutinho 1978). This diversity results from the combined influences of fire, seasonality, and heterogeneous soil conditions (Furley & Ratter 1988; Pinheiro & Monteiro 2010). In the cerrado *sensu stricto*, a typical savanna formation, scattered trees and shrubs coexist with a high richness and abundance of grass species, and fire plays a central role in structuring plant communities (Sano et al. 2008).

Seed traits are critical for plant persistence in fire-prone environments. In the cerrado *sensu stricto*, both dormant and non-dormant seeds occur, representing distinct recruitment strategies (Baskin & Baskin 2004; Escobar et al. 2018). While dormant seeds rely on specific cues to initiate germination, non-dormant seeds depend primarily on their ability to tolerate environmental stress and establish when conditions are favorable (Baskin & Baskin 2004). In this context, it is important to note that the role of fire in breaking dormancy in the Cerrado may be more limited than previously assumed, with other factors, such as light and temperature, playing key roles in regulating germination (Thompson & Ooi 2010; Zupo et al. 2021).

During fire events, seeds may be exposed to high temperatures, which can directly affect their survival (Dayamba et al. 2010; Daibes et al. 2018). Non-dormant seeds are generally more susceptible to heat damage or combustion (Ramos et al. 2016), particularly when located in exposed positions. In contrast, seeds protected within fruits or positioned higher in the tree crown may escape lethal temperatures due to structural insulation and reduced heat exposure (Cirne & Miranda 2008; Sato et al. 2018). This spatial and structural heterogeneity in heat exposure creates a gradient of survival conditions, influencing which seeds persist and ultimately contribute to post-fire recruitment.

Heat tolerance is influenced by seed and fruit traits, including coat thickness, moisture content, size, and structural protection (Bicalho et al. 2016; Cirne & Miranda 2008; Ribeiro & Borghetti 2014; Ribeiro et al. 2015; Souza et al. 2021). Although dormant seeds are often more resistant to high temperatures (Ramos et al. 2016; Zironi et al. 2019), some non-dormant species can also withstand heat shocks and germinate after fire (Macedo et al. 2022), indicating a broader range of adaptive strategies than traditionally assumed. This suggests that fire frequency may favor species with heat-tolerant traits; however, the fate and performance of non-dormant seeds under these conditions remain poorly understood.

Exposure to sublethal temperatures, such as those experienced within fruits (*e.g.*, ~70 °C) may be a common condition for seeds dispersed after fire (Palermo 2011). However, surviving such temperatures does not necessarily imply that seeds will maintain similar germination performance compared to unexposed seeds (Macedo et al. 2022). Therefore, understanding germination responses under realistic post-fire temperature fluctuations is essential to determine how these species persist and to identify potential selective pressures shaping community composition in fire-prone environments.

Despite this, non-dormant woody species remain comparatively understudied in fire ecology, particularly regarding the combined effects of heat exposure and post-fire environmental conditions on seed imbibition and germination. Addressing this gap is essential for predicting population persistence in fire-prone environments.

Thus, this study investigates the effects of heat shocks on the imbibition and germination of *Vochysia tucanorum* Mart. (Vochysiaceae) seeds under temperature fluctuations simulating post-fire conditions in the cerrado *sensu stricto*. By focusing on a non-dormant woody species, this study aims to provide a functional perspective on how different seed strategies contribute to persistence in fire-prone environments. We hypothesize that (i) heat exposure at sublethal temperatures does not impair seed imbibition, and (ii) heated seeds exhibit similar germination performance to unheated seeds under temperature fluctuations simulating post-fire conditions.

2 Material and methods

2.1 Plant material and experimental area

Vochysia tucanorum Mart. (Vochysiaceae) is a generalist species that germinates under both light and dark conditions (Barbosa et al. 1999). It is a late-successional woody species with non-dormant and anemochorous seeds, with its fruiting peak occurring in September (Escobar et al. 2018; Landinho et al. 2018). This species is an ideal model for investigating seed performance under temperature fluctuations, as it possesses ecological value in promoting the recruitment of other tree species (Abreu et al. 2021), and is widespread throughout the Cerrado, occurring in both savanna and forest vegetation (Durigan et al. 2003).

Seeds of *V. tucanorum* were collected in October 2023 at cerrado *sensu stricto* sites within the Santa Bárbara Ecological Station (SBES) (22°41' to 22°46' S and 49°16' to 49°10' W), located in southeastern Brazil. This region has a hot and humid climate with a pronounced dry winter. The dry season extends from May to September, while the rainy season, characterized by concentrated rainfall, occurs from October to April. The annual mean precipitation is between 1100 and 1300 mm, and the monthly mean temperatures vary between 16 °C and 24 °C (Melo & Durigan 2011).

Seeds were obtained from mature fruits (that are deiscent) that were open or partially open, collected from at least five spatially distant individuals to ensure genetic variability. Only seeds exhibiting uniform coloration and no visible signs of predation or decomposition were selected for the experiment to ensure viability. These seeds were stored in paper bags in a climate-controlled room until the start of the study. The experiments were conducted one month after seed collection.

2.2 Experimental design

A total of 240 seeds of *Vochysia tucanorum* were selected and divided into two groups of 120 seeds each, corresponding to the control and heat shock treatments. Each treatment consisted of six replicates (germination box), with 20 seeds per replicate. Only the seeds in the heat shock treatment were exposed to 70 °C for 5 min. Subsequently, to assess imbibition and germination, all replicates (of the control and

heat shock groups) were moistened and placed in germination chambers, where they remained for 30 days under temperature fluctuations simulating post-fire conditions in the cerrado *sensu stricto* (see below).

2.3 Heat shocks

The experiment simulated temperatures that seeds would experience during a fire event in the tree crown, specifically at heights greater than 1 m. A temperature of 70 °C for 5 min was selected, corresponding to temperatures recorded inside fruits during fires in the Cerrado (Palermo 2011). Seeds were heated using a preheated muffle furnace. To ensure rapid and uniform heat exposure, each replicate was placed in an aluminum container (Paredes et al. 2018). Furthermore, replicates were heated separately to avoid pseudoreplication (Morrison & Morris 2000).

2.4 Temperature fluctuations

Both of control and heat shock treatment seeds were incubated in germination chambers under a controlled light regime (12 h light / 12 h dark) and temperature fluctuations simulating post-fire conditions in the cerrado *sensu stricto*, with the average daily variations recorded in December. These fluctuations were recorded using a HOBO U23—001 thermo-hygrometer (Sigma Sensors, São Paulo, Brazil) at a burned cerrado *sensu stricto* site within the SBES (Fig. 1). December represents the transition between the end of seed dispersal and the onset of increased precipitation (Escobar et al. 2018), conditions that favor seed germination.

2.5 Imbibition

Imbibition curves of the seeds were measured for each treatment. The initial mass of the seeds was measured prior to the heat shock treatment and water exposure. All replicates were placed in germination boxes (13 cm×13 cm×4 cm) covered with their respective transparent plastic lids, lined with filter paper and moistened with 20 mL of deionized water to standardize initial water availability in each replicate.

Water absorption was measured by weighing the seeds after one hour of hydration. The seeds were weighed hourly for the initial 8 h, and again after 12 h

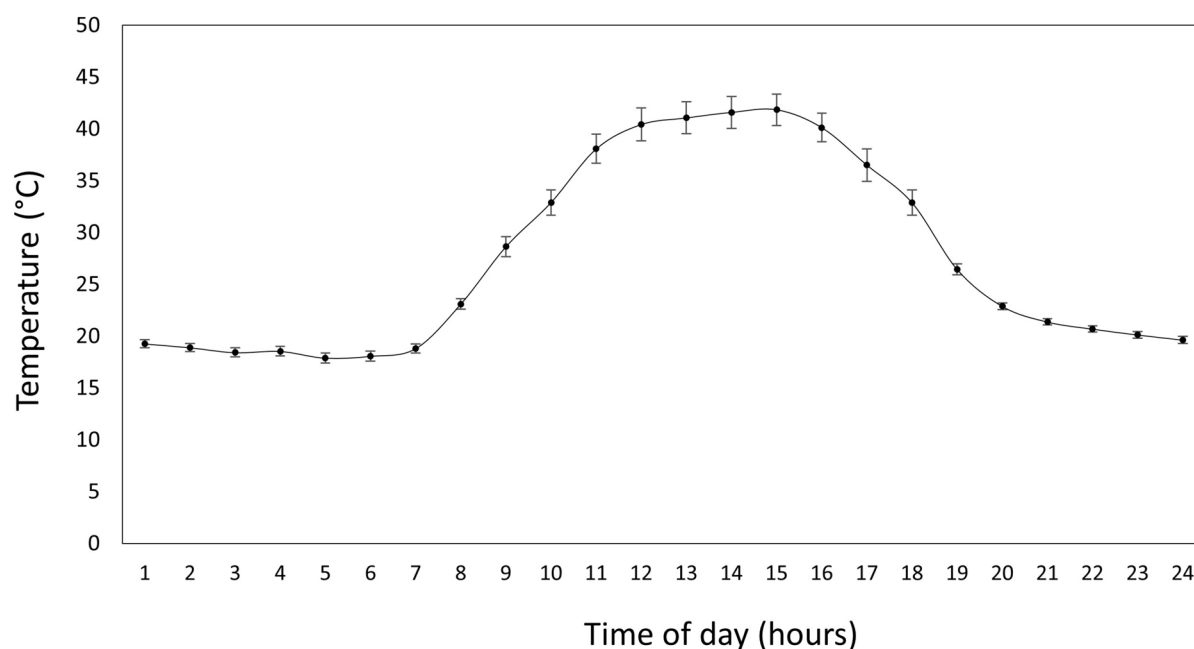


Fig. 1 Temperature profile programmed in the germination chambers during the 30-day seed incubation period. The fluctuations simulate the average daily temperature (°C) recorded

in December at a burned cerrado *sensu stricto* site, Santa Bárbara Ecological Station. Bars are SE

of exposure to deionized water. After establishing the imbibition curve, the seeds were weighed every 24 h for 9 days (216 h). Replicates with germinated seeds were excluded from subsequent weighings; however, their germination continued to be monitored. When necessary, deionized water was added to maintain consistent moisture in the filter paper.

2.6 Germination performance

Germination was monitored for 30 days for each treatment and considered complete upon radicle protrusion and the formation of the geotropic curve (Labouriau et al. 1963). To evaluate the effects of fire on germination traits, Germinability (%G), Mean Germination Time (MGT), and Germination Speed Index (GSI) were calculated.

Germinability (%G) was calculated according to Labouriau (1983):

$\%G = (\sum n_i \cdot N^{-1}) \cdot 100$, where $\sum n_i$ represents the total number of germinated seeds with regard to the number of seeds placed to germinate (N).

Mean Germination Time (MGT) was calculated following Labouriau (1983):

$TMG = \frac{\sum n_i \cdot t_i}{\sum n_i}$, where n_i is the number of germinated seeds in a determined time t_i and t_{i-1} .

Germination Speed Index (GSI) was calculated according to Maguire (1962):

$IVG = \frac{G_1}{N_1} + \frac{G_2}{N_2} + \dots + \frac{G_n}{N_n}$, where G represents the number of germinated seeds and N is the number of days after sowing.

After 30 days, non-germinated seeds were subjected to a Tetrazolium Test (1% buffered solution with pH 7) to assess viability. The seeds were immersed in the solution for 24 h, with viability indicated by red coloration. Seeds lacking this coloration were classified as non-viable (Borghetti & Ferreira 2004). Viability was determined by the percentage of germinated seeds over non-germinated ones.

2.7 Data analysis

Imbibition was analyzed by calculating the mean seed fresh mass per replicate at each hour. Imbibition rates, as well as germination performance (%G, MGT, GSI) were then compared between the treatments (control and heat shock at 70 °C for 5 min). Differences

between the treatments were assessed using a student *t* test ($P < 0.05$).

3 Results and discussion

The imbibition and germination performance under temperature fluctuations simulating post-fire conditions in the cerrado *sensu stricto* were not significantly affected by the heat shocks; consequently, these results support our initial hypotheses.

Prior to imbibition, the fresh mass (mean $\pm$ SE) of control seeds was 0.56 ± 0.008 g, while that of the heat-shocked seeds was 0.57 ± 0.007 g, indicating that the seeds had similar initial mass. Within the first 12 h of imbibition (Fig. 2), both treatments doubled their initial seed mass; this period represents the first phase of the imbibition curve, which is typical for seeds in general (Bradford 1990; Fatokun et al. 2022). During the first 24 h of imbibition (Fig. 3), seeds showed a mass increment of 132% in the control and 126% in the heat shock treatment, therefore, exhibiting close values. Similarly, at the end

of the imbibition period (216 h), the fresh mass was 1.77 ± 0.03 g for the control and 1.80 ± 0.03 g for the heat shock treatment (Fig. 3). Consequently, heated and unheated seeds absorbed water in similar proportions, with no significant differences between them ($t = -0.06$, $df = 36$, $p = 0.94$).

Some non-dormant seeds tolerate and germinate after heat shocks; however, their initial development may be impaired (Macedo et al. 2022). Given that germination begins with seed imbibition (Bewley 1997), evaluating the imbibition of heated and unheated seeds under temperature fluctuations could provide insights into seed performance in post-fire environments. However, our results show that metabolic repair activity and cell growth are maintained similarly in both the control and heat shock treatments (Castro & Hilhorst 2004); therefore, the germinative process were not affected. This suggests that post-germinative processes (seedling development) could be the developmental stage more affected by fire in non-dormant species. Moreover, the inclusion of an imbibition phase analysis after heat shocks and under temperature fluctuations remains scarce in the literature,

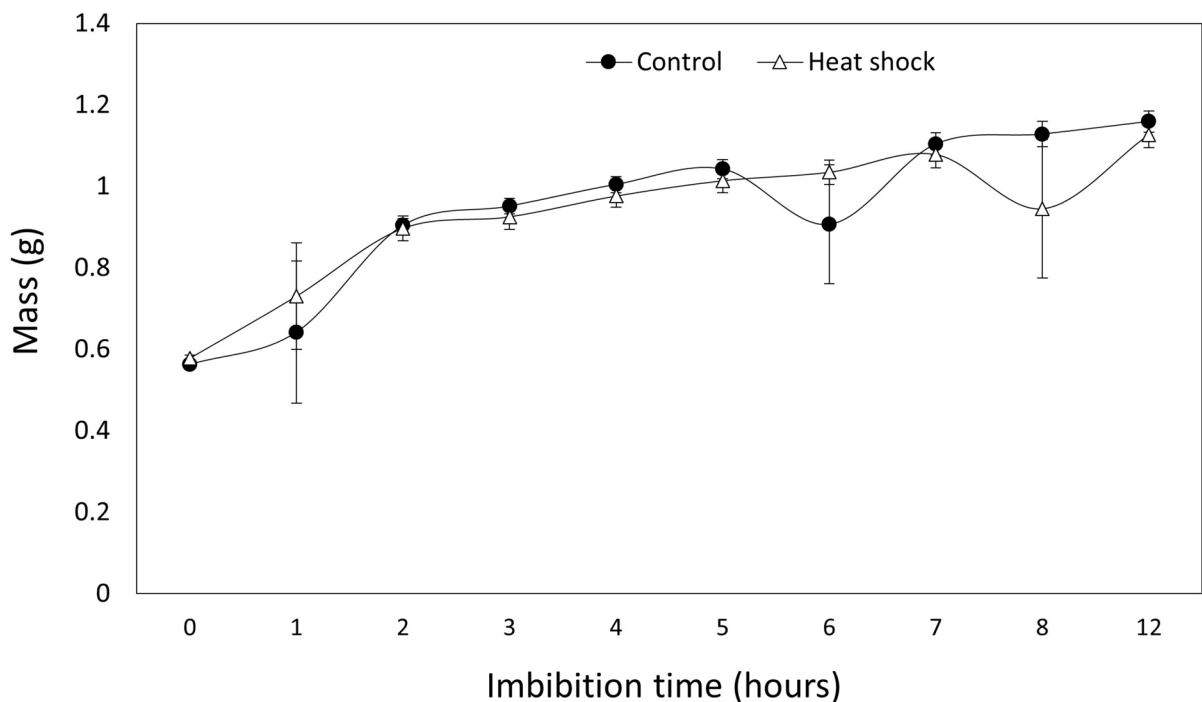


Fig. 2 Fresh mass of *Vochysia tucanorum* Mart. seeds during the first 12 h of imbibition, comparing control and heat shock treatments (70 °C for 5 min). Dots represent mean values

($n = 6$). For each evaluation time (hour), the absence of letters indicates lack of significant differences between treatments by the student *t* test ($P < 0.05$). Bars are SE

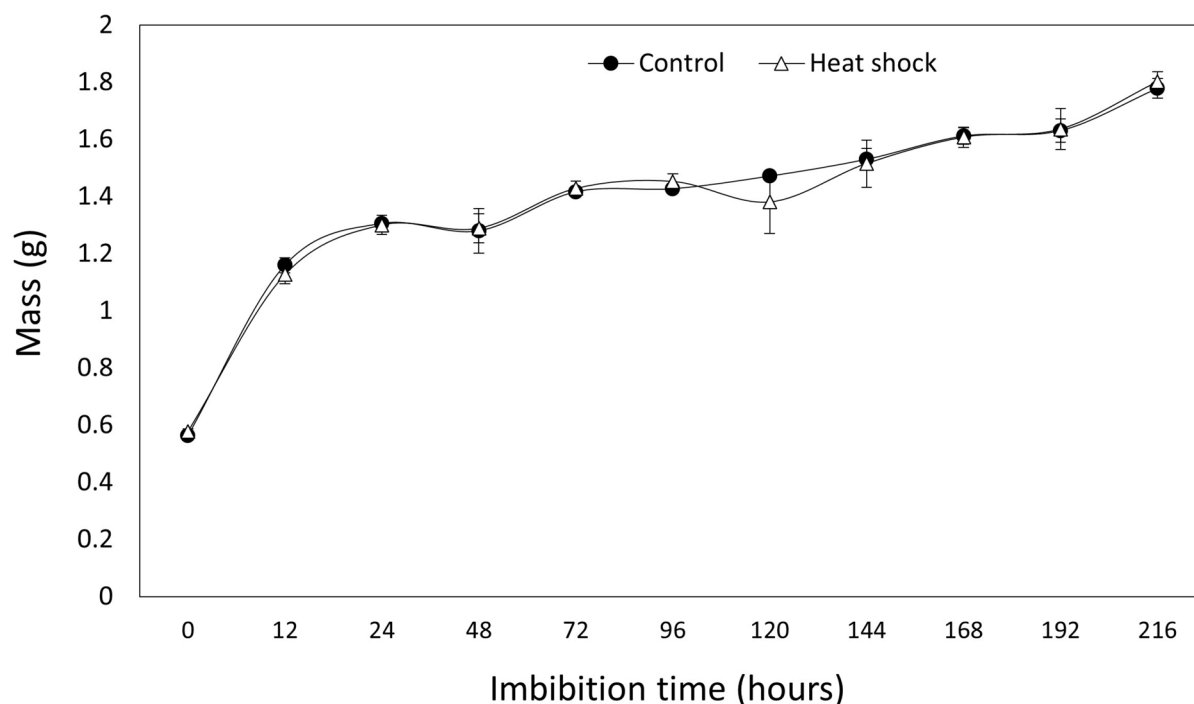


Fig. 3 Fresh mass of *Vochysia tucanorum* Mart. seeds during 216 h of imbibition, comparing control and heat shock treatments (70 °C for 5 min). Dots represent mean values ($n=6$).

For each evaluation time, the absence of letters indicates lack of significant differences between treatments by the student t test ($P < 0.05$). Bars are SE

Table 1 Germination performance of *Vochysia tucanorum* Mart seeds under control and heat shock treatments (70 °C for 5 min)

Germination performance	Control	Heat shock
%G	93.33 ± 3.07	82.5 ± 7.71
MTG	13.25 ± 0.16	13.48 ± 0.8
GSI	1.44 ± 0.06	1.29 ± 0.15
Viability	94.16 ± 0.65%	85.83 ± 1.27%

Data are presented as mean values ($n = 6$) ± S.E. The absence of letters indicates no significant differences between treatments by student t test ($P < 0.05$)

underscoring the importance and novelty of this contribution in addressing existing knowledge gaps.

In line with these results, %G, MGT, and GSI (Table 1) did not differ significantly between the control and heat shock treatments, with $t = -1.30$, $df = 10$, $p = 0.22$; $t = 0.28$, $df = 10$, $p = 0.78$; $t = -0.87$, $df = 10$, $p = 0.40$, respectively. Although germination in the control group began six days after moistening, while heat-shocked seeds began on the ninth day, this initial

delay did not result in significant differences in the overall germination parameters.

Some seeds exhibit optimal and limiting temperatures for germination, allowing them to germinate in both the presence and absence of fire (Gashaw & Michelsen 2002). Optimal and limiting temperatures for germination of *V. tucanorum* seeds were not investigated in the present study, but germination under the presence and absence of heat shocks simulating fire passage was observed in *V. tucanorum* and reported in other non-dormant woody species (Ribeiro et al. 2012; Dayamba et al. 2008). Additionally, fruits can play a critical role in ensuring that non-dormant seeds remain within this temperature range during fire events. For instance, during a prescribed fire where maximum external temperatures reached 393 to 734 °C, the internal temperature of *Kielmeyera coriacea* (Calophyllaceae) fruits remained between 61 to 63 °C (Cirne e Miranda, 2008). Furthermore, it has been reported that *K. coriacea* seeds germinate after heat shocks of 70 °C (Macedo et al. 2022), which may indicate that the fruits of this species effectively maintain internal temperatures below the lethal threshold

for seeds. On the other hand, seeds of *Qualea parviflora* (another Vochysiaceae species from the Cerrado vegetation) located in fruits higher than 1 m within the tree crown were negatively affected by the passage of fire (Palermo 2011). In that study, the internal fruit temperature was approximately 70 °C, while the external temperature was around 500 °C. Nevertheless, when subjected to 70 °C for 5 min under laboratory conditions, the germination performance of *Q. parviflora* was not affected (Macedo et al. 2022), following the same patterns we observed in the present study. This suggests that, in seeds of Cerrado woody species of this genus, other factors are involved in determining seed viability and germination during a fire in the field, as the timing of fruit opening, humidity, or temperature fluctuations.

The observed thermal resilience, alongside the lack of significant differences in imbibition and germination performance between the control and heat shock groups under temperature fluctuations simulating post-fire conditions in the cerrado *sensu stricto*, suggests that *V. tucanorum* seeds adopt a “fire-tolerant” rather than a “fire-stimulated” or a strictly “fire-dependent” strategy (Paula & Pausas 2008; Newton et al. 2021). This may facilitate consistent recruitment under both the presence and absence of fire in post-fire environments, supporting population stability across different scenarios. This ability may be considered a strategy to occupy newly emerging niches following fire events (Coutinho 1977; Nolan et al. 2021). Nevertheless, to better understand the capacity of heated and unheated *V. tucanorum* seeds to colonize niches in post-fire environments, it is necessary to evaluate their seedling development under those conditions.

Although viability (Table 1) did not differ significantly between treatments ($t = -1.16$, $df = 10$, $p = 0.27$), approximately 15% of *V. tucanorum* seeds were damaged in the heat shock treatment. This outcome may be attributed to the production of heterogeneous seeds, which exhibit genetic and physiological variability, a strategy commonly adopted by higher plants to enhance survival under diverse ecophysiological conditions (Matilla et al. 2005). As a result, a single plant may produce seeds that are either tolerant or susceptible to heat shock. Seed heteromorphism represents a crucial bet-hedging strategy, allowing the species to spread its reproductive risk across unpredictable environmental conditions, ensuring that at

least a portion of its progeny will survive and germinate (Imbert 2002; Gianella et al. 2021). Therefore, conservation and restoration strategies in fire-prone environments should consider not only the overall resilience of a species but also the intraspecific variability in seed traits, which can influence the effectiveness of seed-based interventions. Nevertheless, the successful establishment of seedlings in the field is a multifaceted process influenced by complex interactions between abiotic factors such as temperature, light, humidity, and fire (Cardoso 2004), as well as biotic factors, including competition and predation (Janzen 1971; Davis et al. 1998).

Several studies have shown that fire can either promote or exclude species (Rawitscher 1948; Durigan 2020), but its specific role in the recruitment of species across different functional groups remains unclear.

The present study demonstrated that heat shocks of 70 °C for 5 min do not impair imbibition or germination in *V. tucanorum* seeds under conditions simulating post-fire conditions in the cerrado *sensu stricto*. This ensures seed survival and germination in post-fire environments. Thus, a broader range of temperatures and heat shock durations should be tested to better understand this species' tolerance to fire. Furthermore, expanding germination research to encompass a wider range of interacting environmental factors will be essential to refining predictions of seed persistence and regeneration in fire-prone and post-fire environments.

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Author Contributions JZM: Data collection, experiment execution, statistical analysis, and manuscript drafting. MAM: Experimental design, support with data collection, and manuscript revision.

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Data availability The data supporting this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no conflicts of interest.

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