Acta Botanica Brasilica, 2026, 40: e20250124
doi: https://doi.org/10.1590/1677-941X-ABB-2025-0124

Original Article

Seeds of ruderal Cerrado legumes tolerate fire-related temperatures and may release dormancy after heat exposure

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ABSTRACT

Seed dormancy and heat tolerance are critical traits for plant persistence and regeneration in fire-prone ecosystems. In this study, we evaluated the effects of fire-simulated heat shocks on seed germination and survival in seven legume species from degraded areas of the Cerrado, aiming to identify strategies that may facilitate species establishment in these environments. Seeds were exposed to a range of heat treatments (60–200 °C for 1, 3, and 5 minutes) simulating natural fire conditions. Overall, the species exhibited high tolerance to elevated temperatures, with all of them tolerating up to 200°C for 1 minute. Heat-stimulated dormancy release occurred in five species (*Chamaecrista flexuosa*, *C. ramosa*, *Crotalaria pallida*, *Mimosa dolens*, and *M. xanthocentra*). However, in most cases, more than half of the seeds remained dormant after heat exposure, suggesting that higher temperature thresholds or additional environmental cues are required to break dormancy. Taken together, these results indicate that in ruderal Cerrado legumes, the combination of high heat tolerance and some degree of heat-stimulated dormancy release may contribute to their successful establishment and persistence in frequently burned and degraded Cerrado environments.

Keywords: Fabaceae, physical dormancy, heat shock, seed survival, tropical savanna.

Received July 09, 2025; Accepted June 25, 2026
Editor-in-Chief: Thaís Elias Almeida; Associate Editor: Marco Sarigu

How to cite:
Ribeiro JWF, Bailon RM, Kolb RM. 2026. Seeds of ruderal Cerrado legumes tolerate fire-related temperatures and may release dormancy after heat exposure. Acta Botanica Brasilica 40: e20250124. doi: 10.1590/1677-941X-ABB-2025-0124

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Introduction

Fire regimes are among the main ecological drivers shaping plant communities worldwide (Bond *et al.*, 2005; Lehmann *et al.*, 2011). In fire-prone ecosystems, vegetation has co-evolved with recurrent fires over millions of years, leading to the development of diverse adaptive traits that enhance post-fire plant regeneration (Pausas & Keeley, 2009). These traits include resprouting from below-ground organs, recruitment from heat-tolerant seeds, or a combination of both (Keeley *et al.*, 2011; Pilon *et al.*, 2021; Zupo *et al.*, 2021). In impermeable-seeded species, extreme temperatures during fires can break physical dormancy, cuing germination to postfire conditions when light, water, and nutrient resources are abundant (Keeley *et al.*, 2011; Pausas & Lamont, 2022). Understanding seed responses to fire-related temperatures is essential for explaining recruitment patterns and species distribution in fire-prone environments, particularly in the context of emerging novel fire regimes (Schmidt & Eloy, 2020; Segura-Garcia *et al.*, 2025).

Fire-related heat shocks can break physical dormancy by disrupting the water-impermeable palisade cells of the seed coat (Baskin *et al.*, 2000). However, exposure to extreme temperatures during fires can strongly reduce seed survival. Seed survival depends on species-specific thermal thresholds; short exposures to temperatures above 100°C can markedly reduce survival in fire-sensitive species, whereas seeds of more tolerant species may survive temperatures up to 200°C (Ribeiro & Borghetti, 2014; Ooi *et al.*, 2014). Even though direct exposure to heat during fires can increase mortality, buried seeds may experience lower mortality because soil acts as a thermal insulator (Daibes *et al.*, 2017; Zupo *et al.*, 2022). The balance between heat tolerance and dormancy release determines whether seeds persist in the soil seed bank or germinate after fire (Pausas & Lamont, 2022).

Heat-stimulated dormancy release is common among impermeable-seeded species in woody ecosystems with crown-fire regimes, including Mediterranean and other warm-temperate ecosystems (Bell *et al.*, 1992; Moreira *et al.*, 2010; Moreira & Pausas, 2012; Pausas & Lamont, 2022). In Mediterranean-type ecosystems, where crown fires are typically intense, fire can cause high mortality even among resprouting species (Lloret & López-Soria, 1993). Under such conditions, population persistence may depend on the successful recruitment of new individuals after fires to compensate for fire-induced mortality (Pausas & Keeley, 2014). In the Cerrado, where surface fires are frequent but typically low in intensity, most species can recover through post-fire resprouting (Pilon *et al.*, 2021; Zupo *et al.*, 2021), with heat-stimulated dormancy release less frequent than in other fire-prone ecosystems (Fichino *et al.*, 2016; Zupo *et al.*, 2016; Daibes *et al.*, 2019; Zupo *et al.*, 2021; Pausas & Lamont, 2022).

In the Cerrado, Fabaceae is the most representative family with physical dormancy, often producing impermeable seeds that survive surface fire temperatures of 100°C but do not have their dormancy released by heat (Daibes *et al.*, 2019; Zupo *et al.*, 2021). Natural fires in the Cerrado are typically low-intensity surface fires that rapidly spread through the continuous C_4 grass layer, often occurring at intervals of 3 to 4 years (Coutinho, 1982; Miranda *et al.*, 1993). These fires predominantly occur during the transitional periods between wet and dry seasons or during the wet season, frequently ignited by lightning during thunderstorms (Ramos-Neto & Pivello, 2000). During Cerrado fires, soil-surface temperatures above 100°C may last for 1–3 minutes, whereas the highest peaks (200–400°C) typically persist only for a few seconds. Conversely, at 1 cm depth, temperatures rarely exceed 100°C (Miranda *et al.*, 1993; Daibes *et al.*, 2017; Zupo *et al.*, 2022). However, the fire regimes in the Cerrado have changed, with most fires now originating from human activities rather than natural causes (Pivello *et al.*, 2025; Segura-Garcia *et al.*, 2025). Anthropogenic fires, which are very frequent (every 2 to 3 years) and distributed throughout the dry season, are typically more intense and cause serious damage to fire-sensitive vegetation (Schmidt & Eloy, 2020; Segura-Garcia *et al.*, 2025). Moreover, the presence of invasive grasses in degraded Cerrado environments may further increase fire intensity and duration, owing to the greater accumulation of fuel biomass (D'Antonio & Vitousek, 1992; Gorgone-Barbosa *et al.*, 2015; Rossi *et al.*, 2014).

Across the Cerrado, some Fabaceae species may be considered ruderal (*sensu* Frenkel, 1977; Aronson *et al.*, 2011), as they are broadly distributed and tend to occupy and proliferate in human-modified, highly degraded habitats such as roadsides and abandoned pastures, where anthropogenic fires are frequent (Vasconcelos *et al.*, 2014; Durigan *et al.*, 2018). Their persistence in highly degraded fire-prone environments can suggest a selection for fire-resistant propagules that can survive repeated burns (Ruprecht *et al.*, 2013). In frequently burned, degraded Cerrado sites, species often display functional traits that confer tolerance to recurrent fire, enabling their persistence and dominance under such conditions (Vasconcelos *et al.*, 2014). However, whether this success reflects high seed heat tolerance, fire-stimulated dormancy release, or both, remains poorly understood. Addressing this question is crucial for interpreting their ecological strategies and the mechanisms underlying natural regeneration in degraded tropical environments.

Here, we tested the effects of fire-simulated heat shocks on seed germination and survival of seven ruderal legume species abundant in degraded areas of Cerrado. We focused on two key seed traits related to fire resistance: heat-stimulated dormancy release and heat tolerance. Specifically, we asked: (i) Are fire-related temperatures sufficient to promote dormancy release and germination

in these species? and (ii) How do fire-related temperatures affect seed survival? Although Daibes *et al.* (2019) found that most Fabaceae species from natural Cerrado sites did not show increased germination and experienced high mortality under the most extreme heat shocks (200ºC), we expected that ruderal species occurring in degraded and frequently burned environments could exhibit distinct responses. Their persistence in such fire-prone environments may indicate enhanced seed tolerance, fire-stimulated dormancy release, or both. Therefore, we hypothesized that ruderal species dominant in frequently burned, degraded habitats would exhibit high seed survival after heat exposure and some level of enhanced germination, thereby contributing to their successful establishment in fire-prone, degraded environments.

Material and methods

Seed collection and study area

We collected pods of seven legume species in 2016 and 2017 from degraded areas in and around the Assis State Forest (ASF, 22°35′43.7″ S, 50°24′46.9″ W), São Paulo State, Brazil, which is a protected area of natural resources (Secretaria do Meio Ambiente, 2007). The pods were collected from at least 10 individuals per species along abandoned pastures and unpaved roadsides, where regular disturbances include vegetation cutting or fire. Only mature (dry) pods were collected (the collection months for each species are listed in Table 1). Seeds were removed from their respective pods and sorted, discarding predated seeds. After screening, the seeds were stored for no longer than 30 days. They were kept in paper bags at 25°C, in a dark environment.

The natural vegetation at ASF comprises a mosaic of sclerophyllous forests and wooded savannas on well-drained soils, along with swamp forests and wet grasslands in the riparian zones. Within ASF, native vegetation coexists with forestry plantations (mainly pine) and abandoned pastures (Secretaria do Meio Ambiente, 2007). The region has elevations ranging from 500 to 588 m, with a Cwa climate according to Köppen's classification (Alvares *et al.*, 2013). Annual rainfall is approximately 1,400 mm, with most precipitation occurring during the summer months (December to March) and a dry season in the winter (July to September). The average annual temperature is 21.8°C, with an average minimum of 8.4°C and an average maximum of 32.4°C (Secretaria do Meio Ambiente, 2007). Soil is predominantly sandy, with high aluminum concentrations and low nutrient availability (Juhász *et al.*, 2006).

Study species

Seven Fabaceae species were selected for this study (Table 1). *Bauhinia holophylla* (= *B. rufa*) is the only species endemic to the Cerrado domain (Vaz & Santos, 2025), whereas the others are widely distributed across South America, occurring in different regions of the Cerrado and adjacent biomes (Fig. 1A-G). The seven studied species include different growth forms (herbs, subshrubs, and shrubs) and typically occur at low densities in well-preserved Cerrado grasslands and savannas but frequently occur in anthropogenically degraded habitats (Durigan *et al.*, 2018),

Table 1. Studied species of Fabaceae from the Cerrado. Collection month: the month when mature seeds were collected. Growth form: H – herb; Ss – subshrub; S – shrub. Habitat: G – grassland; S – savanna; D – degraded habitats (e.g., roadsides, abandoned pastures). Dry mass: average (± standard error) of seed dry mass obtained from 100 oven-dried seeds per species. Voucher numbers refer to reference specimens deposited in the Herbarium "Maria Eneyda Pacheco Kauffmann Fidalgo" (SP), Instituto de Pesquisas Ambientais, São Paulo, Brazil. Growth form and habitat were classified according to Durigan *et al.* (2018).

Species	Collection month	Growth form	Habitat	Dry mass (mg)	Voucher
Bauhinia holophylla (Bong.) Steud.	Feb 2017	S	G, S, D	145.3 ± 2.3	SP1377
Chamaecrista desvauxii var. *latistipula* (Benth.) G.P. Lewis	Dec 2016	S	D	7.4 ± 0.2	SP48470
Chamaecrista flexuosa (L.) Greene	Jan 2017	H, Ss	G, S, D	6.8 ± 0.1	SP13187
Chamaecrista ramosa var. *parvifoliola* H.S. Irwin & Barneby	Mar 2016	Ss	G, D	5.8 ± 0.1	SP111889
Crotalaria pallida var. *obovata* (G. Don) Polhill	Jan 2017	H, Ss	G, S, D	2.8 ± 0.03	SP218069
Mimosa dolens var. *rigida* (Benth.) Barneby	Feb 2017	S, Ss	G, S	8.9 ± 0.20	SP217159
Mimosa xanthocentra Mart.	Feb 2017	Ss	G, S, D	4.4 ± 0.7	SP313148

such as abandoned pastures and roadsides (Fig. 1H-J). *Crotalaria pallida* is a short-lived perennial species, which is a naturalized exotic species with origins in tropical Africa and Asia. All study species exhibit physical dormancy, a common trait among Fabaceae genera such as *Bauhinia*, *Chamaecrista*, *Crotalaria*, and *Mimosa* (Williams *et al.*, 2003; Alves *et al.*, 2004; Daibes *et al.*, 2019; Zupo *et al.*, 2021). Taxonomic identification of the studied species was based on herbarium specimens deposited at the Herbarium of the Instituto de Pesquisas Ambientais (Herbário SP – "Maria Eneyda Pacheco Kauffmann Fidalgo"), and the reference voucher numbers are included in Table 1. To determine seed mass, seeds were oven-dried at 80°C for 48 hours (when they reached a constant weight). Subsequently, the dry mass of individual seeds (n = 100 per species) was determined using a precision balance (± 0.1 mg). The resulting data are presented in Table 1.

Heat shock treatments

We performed experimental heat shocks under controlled laboratory conditions and subjected seeds to 10 treatments:

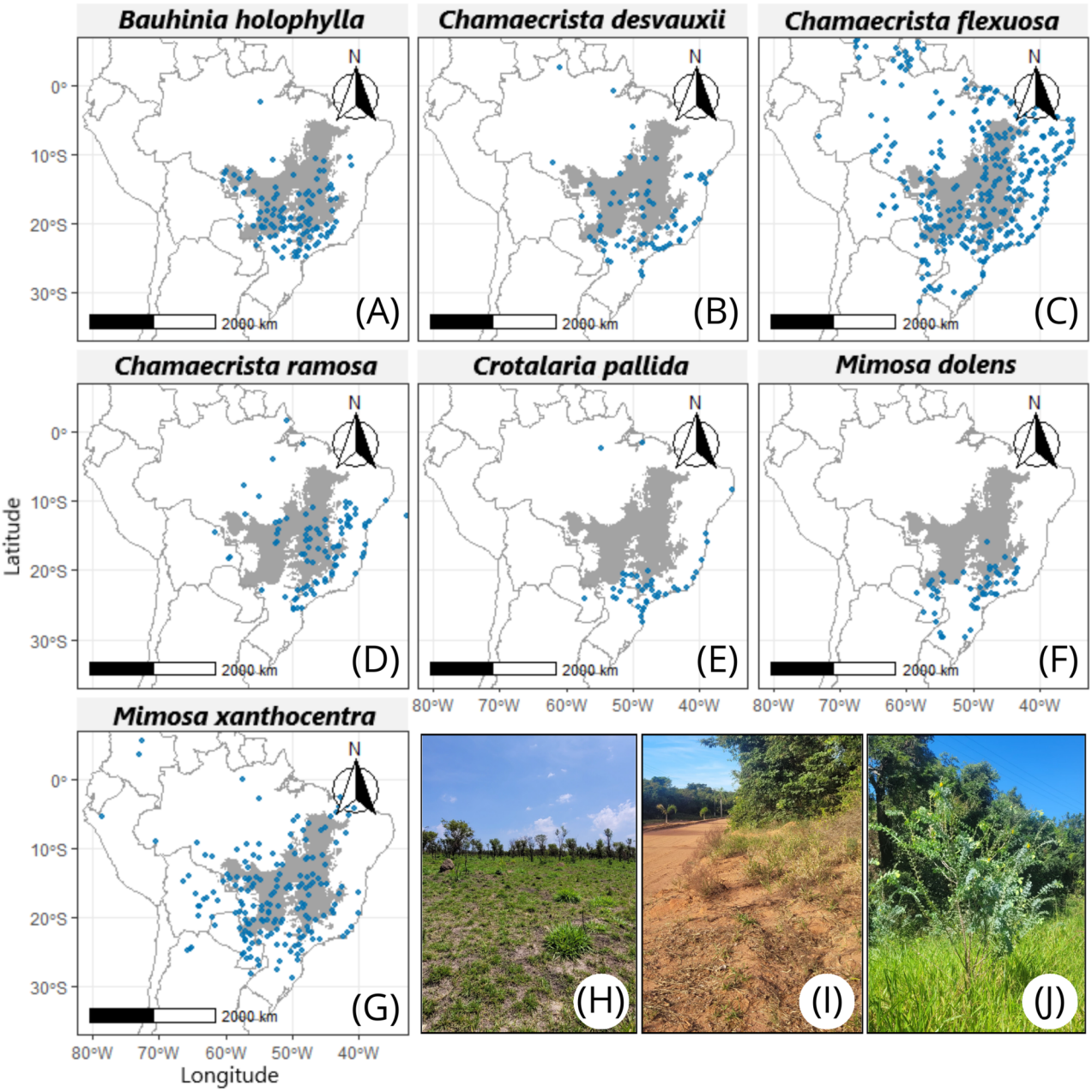


Figure 1. Occurrence records of the seven studied Fabaceae species in South America (A–G) and examples of degraded habitats where they occur (H, abandoned pasture; I-J, roadsides). Blue dots represent georeferenced records obtained from the speciesLink database (https://specieslink.net/). The Cerrado domain is shown in grey according to the WWF terrestrial ecoregions (Olson *et al.*, 2001).

(1) a control group (untreated seeds); (2) 60°C for 1 minute; (3) 100°C for 1 minute; (4) 150°C for 1 minute; (5) 200°C for 1 minute; (6) 60°C for 3 minutes; (7) 100°C for 3 minutes; (8) 150°C for 3 minutes; (9) 200°C for 3 minutes and (10) 200°C for 5 minutes. We applied heat treatments in a pre-heated muffle (Model Economic, EDG Equipment, Brazil). To ensure that seeds were exposed only to the target air temperature, they were placed in porcelain crucibles to avoid direct contact with the bottom muffle surface, which is naturally hotter than the air inside the equipment. We selected temperature levels and exposure times based on fire temperature records reported for Cerrado ecosystems. The 60°C treatment simulates typical temperatures at a depth of 1 cm belowground, which can usually range from 43 to 73°C, depending on the fuel load (Zupo *et al.*, 2022). The higher temperatures (100, 150, and 200°C) reflect aboveground fire conditions, where air temperatures may range from 289 to 395°C near the ground depending on the fuel load (Zupo *et al.*, 2022). We did not test temperatures above 200°C because 200°C is often reported as the threshold for seed mortality under direct fire exposure (Daibes *et al.*, 2018). Exposure durations of 1 and 3 minutes correspond to the average residence times of soil temperatures exceeding 60°C, at –1 cm (0.4–1.9 minutes) and 0 cm depth (4.1–4.4 minutes), and exceeding 100°C at the soil surface (2.3–3.0 minutes), as recorded in natural Cerrado areas (Zupo *et al.*, 2022). We also included a 200°C for 5 minutes treatment to simulate an extreme heat pulse rarely observed under natural conditions, but useful for identifying the upper thermal limits of seed tolerance and the threshold between dormancy release and mortality. However, this treatment was not applied to *C. flexuosa* and *C. ramosa* due to the insufficient number of seeds available.

Germination and viability procedures

After the heat shock treatments, we placed seeds in germination boxes (11 × 11 × 3.5 cm) on a double layer of filter paper moistened with distilled water. Boxes were incubated in germination chambers at an alternating temperature of 20/30°C with a 12-h photoperiod (20W fluorescent lamps, approximately 60 μmol m^{-2} s^{-1}). This alternating temperature regime reflects the typical daily fluctuations in air and soil temperatures observed in our study area (Ribeiro & Kolb, 2016). We used four replicates of 25 seeds per treatment for each species, and germination was monitored daily for 30 days. We counted and removed germinated seeds from the germination boxes at each observation, considering radicle emergence as the indicator of germination. Boxes were randomly arranged in the germination chambers and repositioned at each observation. We replaced filter papers whenever visual signs of fungal contamination were detected. Seeds that remained dormant (i.e., did not imbibe water) at the end of the trials were mechanically scarified with fine nail files and incubated for an additional 30 days under the same germination conditions. Seeds that germinated during this period were considered to have survived the heat treatments and were considered viable. The imbibed but ungerminated seeds were visibly non-viable, showing rotten internal tissues; thus, we did not perform tetrazolium testing.

Data analyses

To test whether fire-related temperatures were sufficient to promote dormancy release and germination of non-scarified seeds, we assessed germination percentage and mean germination time for each replication and treatment. Germination percentage (G%) was determined as the proportion of germinated seeds (ni) relative to the total number of seeds placed to germinate (N) ($G\% = (\Sigma ni / N) \times 100$). Mean germination time (MGT) was determined by dividing the sum of the daily counts of germinated seeds (ni) multiplied by the corresponding incubation day (*ti*) by the total number of germinated seeds (Σni) ($MGT = \Sigma(ni \times ti) / \Sigma ni$) (Ranal & Santana, 2006). We tested differences in G% and MGT between each treatment and the control (untreated seeds) using generalized linear mixed models (GLMs). For G%, we used a binomial distribution (proportion data). For MGT, we used a gamma (with the log link function) distribution. Because GLMs with gamma distribution require strictly positive values, we added a constant (+2) to all MGT values to avoid zero or negative values.

To evaluate whether seeds tolerate fire-related temperatures, we assessed seed viability for each replicate and treatment. Seed viability (SV%) was defined as the sum of the seeds that germinated without mechanical scarification (*g*), and those that germinated only after mechanical scarification (*gscar*), relative to the total number of seeds placed to germinate (*N*) ($SV\% = ((\Sigma g + \Sigma gscar) / N) \times 100$). Differences in SV% between treatments were tested separately for each species using GLMs with a binomial distribution.

We performed all GLM analyses in the R environment (version 4.1.1; R Core Team, 2018). GLMs were performed separately for each species, and the experimental treatments were treated as fixed factors. When the treatment showed no germination, it was removed from the analysis. To perform all GLM models, we used the *lme4* package (Bates *et al.*, 2015). We also used the *DHARMa* package to verify the model adjustments (Hartig, 2022).

Results

Seed germination

Under control conditions (no heat treatment, no mechanical scarification), germination was low, ranging from 3% to 19% across species (Fig. 2). Following heat treatments, germination increased compared to the controls in five species. However, the magnitude of the response

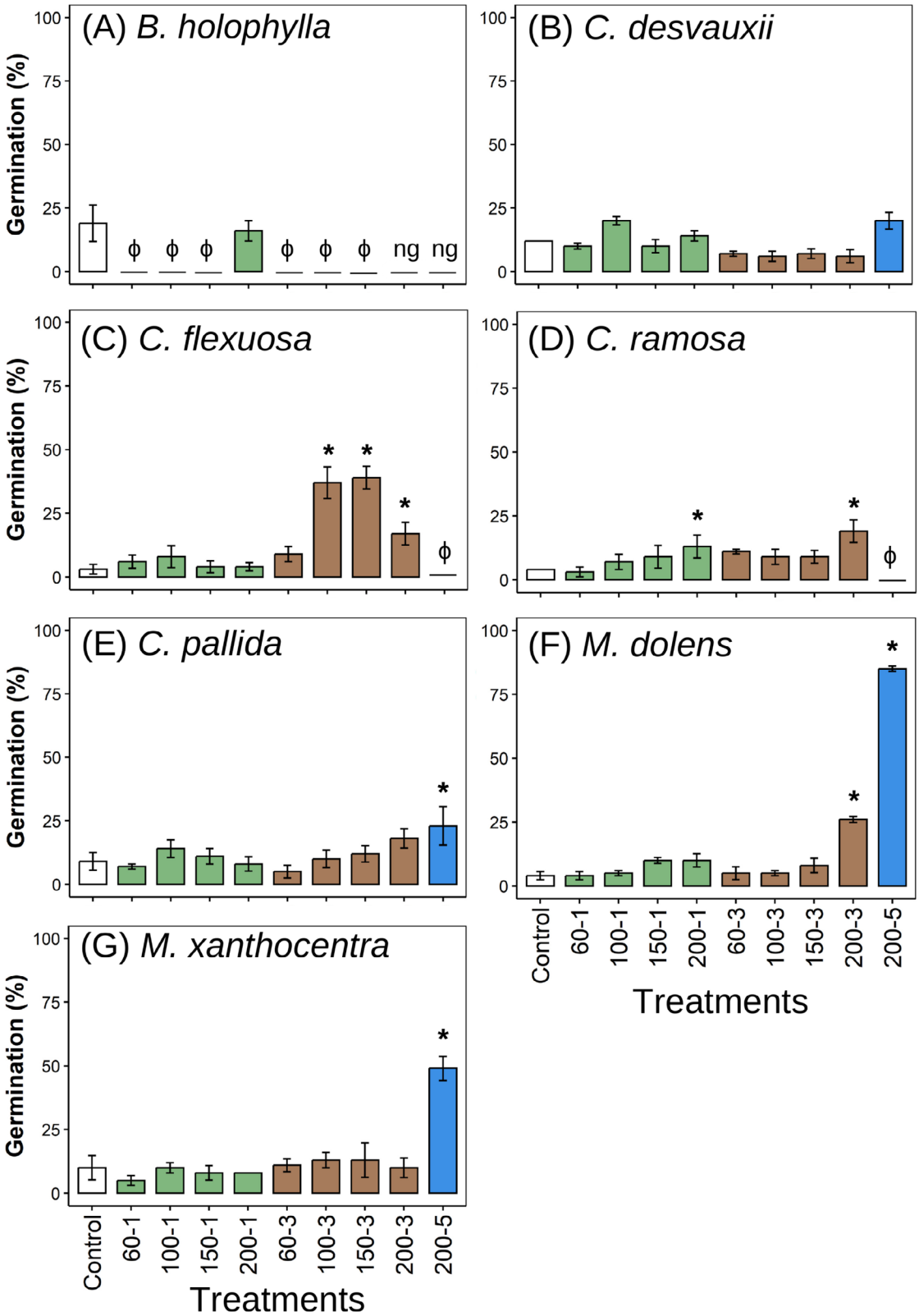


Figure 2. Germination percentage of non-scarified seeds (mean ± SE, n = 4) of seven legume species subjected to heat shock treatments at 60, 100, 150, and 200°C for 1, 3, and 5 minutes, and to a control treatment (no heat exposure). Panels: (A) *Bauhinia holophylla*, (B) *Chamaecrista desvauxii*, (C) *C. flexuosa*, (D) *C. ramosa*, (E) *Crotalaria pallida*, (F) *Mimosa dolens*, (G) *M. xanthocentra*. Asterisks above the bars indicate significant differences compared to the control ($P < 0.05$). ϕ: treatment not performed; ng: no germination recorded.

varied with temperature and exposure duration (Fig. 2, Table S1). In *B. holophylla* seeds, tested only at 200°C, there was no significant difference in germination between heat treatment and control after exposure for 1 minute, and no germination was observed after exposures of 3 or 5 minutes (Fig. 2A). For *C. desvauxii*, germination was unaffected by all tested temperature or exposure time (Fig. 2B). In contrast, *C. flexuosa* showed increased germination compared to the control at 100, 150, and 200°C for 3 minutes, whereas 1 minute exposure had no effect (Fig. 2C). *Chamaechrista ramosa* had a significant increase in germination at 200°C for 1 and 3 minutes, while lower temperatures had no effect (Fig. 2D). For *C. pallida*, germination was similar to the control in most treatments but increased significantly after 200°C for 5 minutes (Fig. 2E). Seeds of *M. dolens* showed a slight increase in germination after 3 minutes at 200°C and a great increase after 5 minutes at 200°C compared to the control (Fig. 2F). *Mimosa xanthocentra* exhibited enhanced germination at 200°C for 5 minutes, while other treatments had values comparable to the control (Fig. 2G).

Mean germination time

Under control conditions, the mean germination time (MGT) ranged from 3.3 to 20.3 days across species (Fig. 3). The heat treatments had minor effects on MGT. Significant changes were seen in only three species (Table S1). The MGT of *B. holophylla*, *C. flexuosa*, *C. ramosa*, and *C. pallida* seeds were unaffected by treatments (Fig. 3A, C, D, and E). In *M. dolens*, MGT increased compared to the control after 150°C by 3 minutes (Fig. 3F). Conversely, heat shocks at 60°C for 1 minute and 200°C for 5 minutes significantly reduced MGT in *C. desvauxii* (Fig. 3B), while in *M. xanthocentra,* only the 200°C for 5 minutes treatment had this effect (Fig. 3G).

Seed viability

Seed viability in the control was high in most species (>75%), except for *B. holophylla* which showed mean seed viability of 48% (Fig. 4). In *B. holophylla*, which was tested only at 200°C, seed viability did not differ from the control in seeds exposed for 1 minute, whereas seeds exposed for 3 or 5 minutes were completely killed (Fig. 4A; Table S2). Heat treatments increased seed viability compared to the control in six species (Table S2): *C. desvauxii* (200°C for 1 minute), *C. flexuosa* (150°C for 1 and 3 minutes), *C. ramosa* (60 and 200°C for 3 minutes), *C. pallida* (60°C for 3 minutes, 150°C for 3 minutes, and 200°C for 3 and 5 minutes), *M. dolens* (200°C for 1 and 3 minutes), and *M. xanthocentra* (100°C for 1 minute, 150°C for 1 and 3 minutes, and 200°C for 1, 3, and 5 minutes) (Fig. 4B-G). We also observed a negative effect on the seed viability of *C. desvauxii* seeds compared to the control when exposed to the 200°C treatment for 5 minutes (Fig. 4B).

Discussion

Our results show that five species exhibited increased germination after at least one of the nine heat treatments, indicating that heat can act as a dormancy-breaking cue. These findings contrast with broader ecological patterns reported for the Cerrado, where heat-stimulated dormancy release is relatively uncommon among legume species typical of well-preserved areas (Fichino *et al.*, 2016; Zupo *et al.*, 2016; Daibes *et al.*, 2019; Zirondi *et al.*, 2019). Three species (*C. flexuosa*, *C. ramosa*, and *M. dolens*) exhibited partial dormancy release after heat exposures of 100–200°C for 1–3 minutes, a temperature range consistent with soil-surface conditions during Cerrado fires (Daibes *et al.*, 2017; Zupo *et al.*, 2022). However, more than half of their seeds remained dormant after these heat exposure treatments, suggesting that other temperatures and/or times of exposure could release seeds from dormancy. For example, seeds of some Mediterranean species require longer exposure times (~5 minutes) to overcome physical dormancy (Moreira *et al.*, 2010). Consistent with this, the longer exposure used to determine upper thermal limits (200°C for 5 minutes) induced dormancy release in two species that showed no response to shorter heat exposures (*C. pallida* and *M. xanthocentra*).

Although heat-induced dormancy release was relatively low in our study, it may still enhance seedling recruitment after fire, when resources are abundant, and competition is reduced (Kotze, 2013; Pausas & Lamont, 2022). However, only recently dispersed seeds that have not been incorporated into the soil seed bank at the time of fire are likely to be stimulated at 200°C, as temperatures at 1 cm depth rarely surpass 100°C (Zupo *et al.*, 2022). In contrast, none of the heat treatments promoted dormancy release and germination in *B. holophylla* and *C. desvauxii*, suggesting that other temperatures or time exposure and/or other environmental cues are required to break dormancy (Pausas & Lamont, 2022).

In addition to direct effects of heating on dormancy release, fire can open gaps in the vegetation, exposing seeds at the soil surface to elevated temperatures and wide daily fluctuations (*e.g.*, 18–53°C; during the dry season), which may help to alleviate physical dormancy in Fabaceae species, as observed for the Cerrado shrubs *M. leiocephala* and *Harpalyce brasiliana* in field experiments (Daibes *et al.*, 2017). Moreover, during the transition from dry to wet seasons, the environment exhibits marked fluctuations in temperature and humidity, even in the absence of fire (Ribeiro & Kolb, 2016). At our study site, bare soil surfaces can reach temperatures of approximately 50°C, particularly in highly degraded microhabitats (Ribeiro, 2014). These conditions may alleviate physical dormancy, promote germination, and enable seedlings to establish at the onset of the following rainy season (Santana *et al.*, 2013;

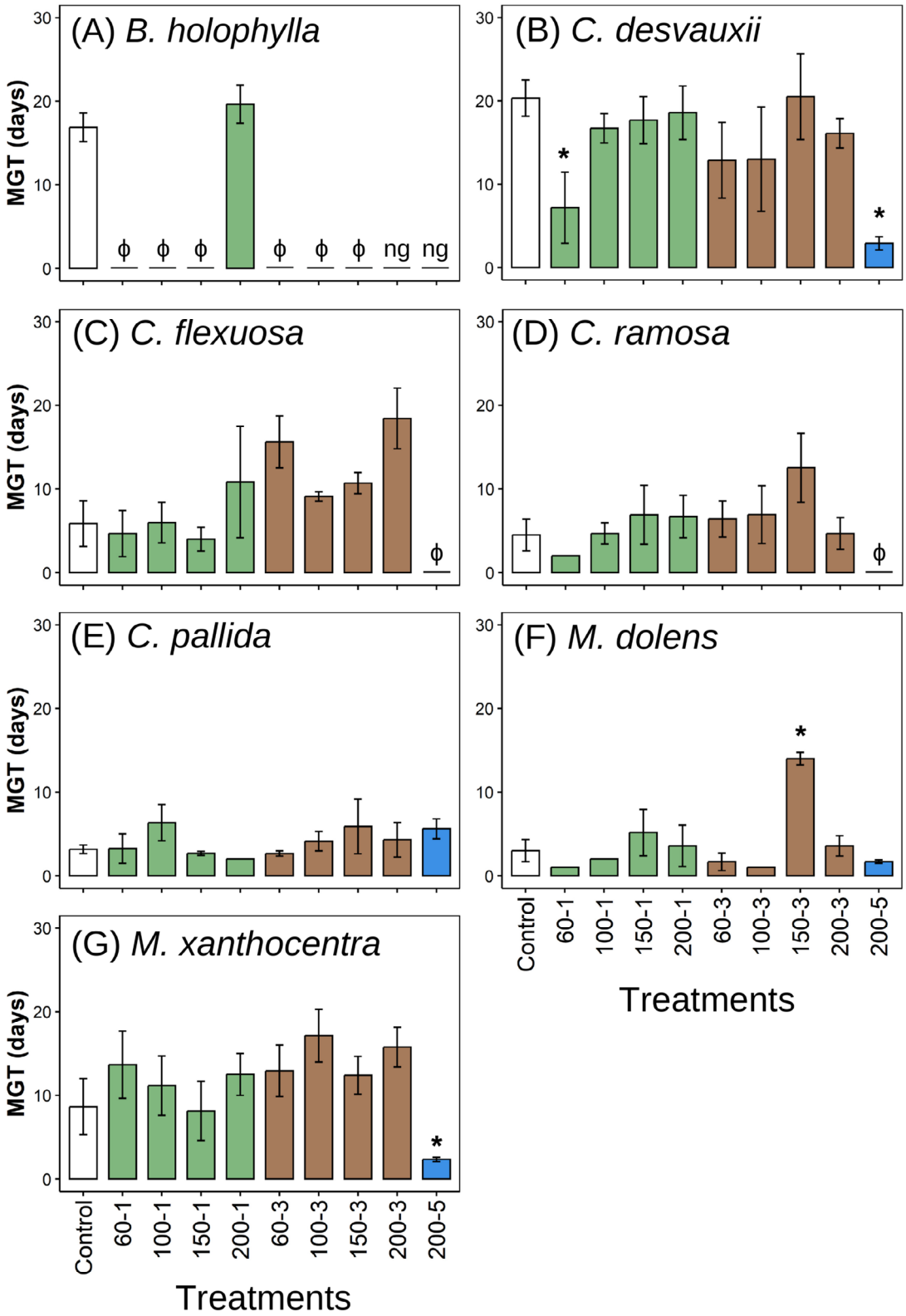


Figure 3. Mean germination time (MGT, mean ± SE, n = 4) of non-scarified seeds of seven legume species subjected to heat shock treatments at 60, 100, 150, and 200°C for 1, 3, and 5 minutes, and to a control treatment (no heat exposure). Panels: (A) *Bauhinia holophylla*, (B) *Chamaecrista desvauxii*, (C) *C. flexuosa*, (D) *C. ramosa*, (E) *Crotalaria pallida*, (F) *Mimosa dolens*, (G) *M. xanthocentra*. Asterisks above the bars indicate significant differences compared to the control ($P < 0.05$). ϕ: treatment not performed; ng: no germination recorded.

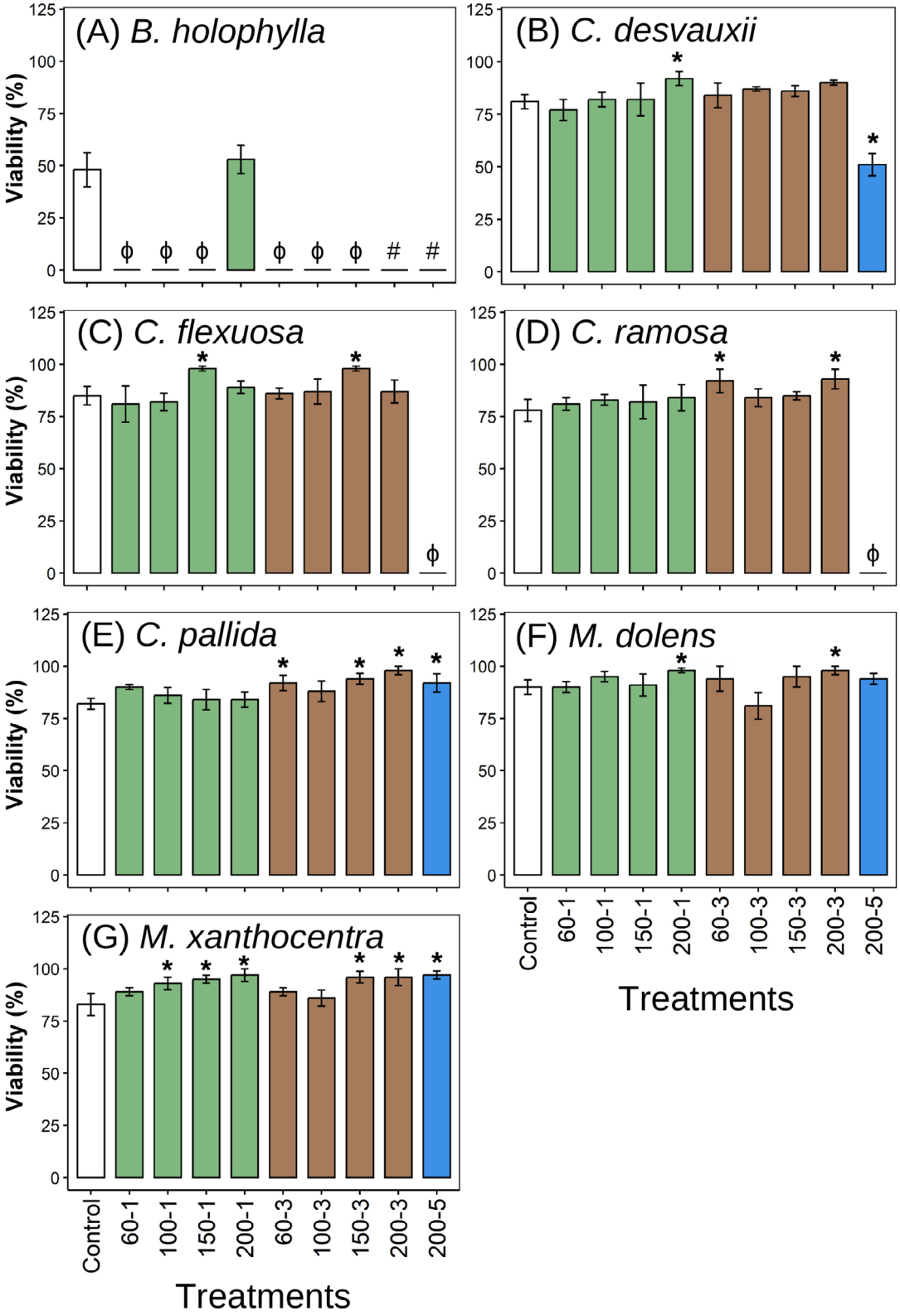


Figure 4. Seed viability (mean ± SE, n = 4) of seven legume species subjected to heat shock treatments at 60, 100, 150, and 200°C for 1, 3, and 5 minutes, and to a control treatment (no heat exposure). Panels: (A) *Bauhinia holophylla*, (B) *Chamaecrista desvauxii*, (C) *C. flexuosa*, (D) *C. ramosa*, (E) *Crotalaria pallida*, (F) *Mimosa dolens*, (G) *M. xanthocentra*. Asterisks above the bars indicate significant differences compared to the control ($P < 0.05$). ϕ: treatment not performed; #: all seeds died. Seed viability represents the total number of seeds that germinated both without mechanical scarification and those that germinated only after mechanical scarification.

Baskin & Baskin, 2014; Zupo *et al.*, 2016). Heat shock had small effects on mean germination time (MGT) compared with its effects on germination percentage. However, *M. dolens* exhibited increased MGT at 150°C for 3 minutes, whereas *C. desvauxii* showed reduced MGT both at 60ºC (1 minute) and 200ºC (5 minutes), and *M. xanthocentra* also displayed reduced MGT at 200°C for 5 minutes. In these cases, the reduction in MGT likely indicates that heat exposure accelerated water uptake and radicle protrusion (Baskin & Baskin, 2014).

Seeds remained viable after exposure to most temperatures and times of exposure, except for *B. holophylla* and *C. desvauxii*, where seed viability decreased under 200°C for 3–5 minutes and 200°C for 5 minutes, respectively. These patterns align with previous studies showing that Cerrado species frequently tolerate short exposures to temperatures up to 200°C (Ribeiro *et al.*, 2013; Daibes *et al.*, 2017; Fidelis *et al.*, 2016). In some cases, seed viability after heat exposure exceeded that of the control; however, this response should be interpreted with caution. One possible explanation is that methodological artefacts associated with manual scarification likely account for this pattern. Specifically, because germination was low in the control treatments, many seeds required scarification, which increased the risk of improper scarification and potential embryo damage, consequently leading to higher apparent mortality. Additionally, reduced fungal growth following heat exposure may partially explain this response, as it could reduce fungal-induced mortality (Bárcenas-Moreno & Bååth, 2009).

Our results show that high heat tolerance is a widespread trait among these legumes, enabling their persistence in the soil seed bank after fire disturbances (Fidelis *et al.*, 2016; Daibes *et al.*, 2017; 2019). This suggests that ruderal legume species may succeed not only through positive germination responses to heat but also through their ability to resist fire temperatures (Fichino *et al.*, 2016; Ocampo-Zuleta *et al.*, 2025). In the degraded areas where they commonly occur, invasion by exotic grasses such as *Urochloa* spp. and *Melinis minutiflora* can lead to the accumulation of large amounts of fine biomass and consequently to hotter fires (D'Antonio & Vitousek, 1992; Rossi *et al.*, 2014; Gorgone-Barbosa *et al.*, 2015), potentially favoring persistence of species with heat-tolerant seeds (Ruprecht *et al.*, 2013).

Finally, the apparent coexistence of resprouting ability and heat-tolerant or heat-stimulated propagules may enhance persistence in frequently disturbed habitats (Frenkel, 1977). Many Cerrado legumes possess underground organs associated with resprouting, as documented for *C. desvauxii* and *C. flexuosa*, and congeners of the other species studied here (Pilon *et al.*, 2021; Zupo *et al.*, 2021; Prochazka *et al.*, 2024). In contrast, the species *C. pallida* has been described as a non-resprouting species after fire, colonizing mainly by seed germination (Pilon *et al.*, 2021). Based on the classification of germinative responses to heat treatments proposed by Paula & Pausas (2008) and Zupo *et al.* (2021), *C. flexuosa*, *C. pallida*, *C. ramosa*, *M. dolens*, and *M. xanthocentra* can be classified as having heat-stimulated propagules, as germination under at least one heat treatment was higher than in the control treatment. In contrast, *B. holophylla* and *C. desvauxii* can be classified as having heat-tolerant propagules, as heated seeds showed germination and viability equal to the control treatment.

Overall, our findings show that ruderal Cerrado legumes combine high seed tolerance to fire temperatures with some degree of heat-stimulated dormancy release. These species disperse their seeds from mid to late rainy season (Tannus *et al.*, 2006), suggesting that seeds released later may remain dormant throughout the dry season (Escobar *et al.*, 2018), with dormancy likely being broken during dry-season fires and germination occurring only when adequate moisture returns at the onset of the rainy season. When paired with widespread resprouting ability, these traits may enhance persistence and recovery after fire, explaining the ecological success of these ruderal legumes in highly degraded and increasingly fire-prone Cerrado landscapes (Vasconcelos *et al.*, 2014).

Acknowledgments

We are grateful to the Instituto de Pesquisas Ambientais do Estado de São Paulo for the research permit at ASF. We thank Daniel Ferreira Chaves and Guilherme Maekawa Casagrande for their assistance during the experimental work. We also thank Dr. Ciro Cesar Zanini Branco and the Laboratory of Aquatic Biology for providing the muffle used in the heat-shock experiments. Finally, we especially thank M.Sc. Pedro Firme da Cruz Júnior for assistance with the experimental work and manuscript revision.

Authors' Contributions

Jonathan Wesley Ferreira Ribeiro: Conceptualization, Formal analysis, Methodology, Visualization, Writing – original draft; **Ramon Monteiro Bailon:** Data curation, Investigation; **Rosana Marta Kolb:** Conceptualization, Methodology, Supervision, Writing – review & editing.

Conflicts of Interest

The authors declare no personal, scientific, commercial, political, or financial conflicts of interest.

Data Availability

The data that support the findings of this study are available upon request from the corresponding author.

Funding Information

No funding was received for this work.

Supplementary Material

The following online material is available for this article:

Table S1. Estimated parameters from generalized linear models (GLMs) for the effect of heat shocks on germination percentage and mean germination time (MGT) in ruderal legumes from the Cerrado.

Table S2. Estimated parameters from generalized linear models (GLM) for the effect of heat shocks on seed viability in ruderal legumes from the Cerrado.

References

Alvares CA, StapeJL, Sentelhas PC, Moraes Gonçalves JL, Sparovek G. 2013. Köppen's Climate Classification Map for Brazil. Meteorologische Zeitschrift 22(6): 711–728. doi: 10. 1127/ 0941- 2948/ 2013/ 0507.

Alves AU, Dornelas CSM, Bruno RLA, Andrade LA, Alves EU. 2004. Superação da dormência em sementes de *Bauhinia divaricata* L. Acta Botanica Brasilica 18: 871–879. doi: 10.1590/S0102-33062004000400018

Aronson J, Durigan G, Brancalion PHS. 2011. Conceitos e definições correlatos à ciência e à prática da restauração ecológica. IF Série Registros 1: 1–38.

Bárcenas-Moreno G, Bååth, E. 2009. Bacterial and fungal growth in soil heated at different temperatures to simulate a range of fire intensities. Soil Biology & Biochemistry 41: 2517–2526. doi:10.1016/j.soilbio.2009.09.010

Baskin CC, Baskin JM. 2014. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. 2 ed. San Diego, Elsevier/Academic Press.

Baskin JM, Baskin CC, Li X. 2000. Taxonomy, anatomy and evolution of physical dormancy in seeds. Plant Species Biology 15: 139–152. doi: 10.1046/j.1442-1984.2000.00034.x

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48. doi: 10.18637/jss.v067.i01

Bell DT, Plummer JA, Taylor SK. 1992. Seed germination ecology in southwestern Western Australia. The Botanical Review 59: 24–73.

Bond WJ, Woodward FI, Midgley GF. 2005. The global distribution of ecosystems in a world without fire. New Phytologist 165: 525–538. doi: 10.1111/j.1469-8137.2004.01252.x

Coutinho LM. 1982. Ecological effects of fire in Brazilian Cerrado. In: Huntley BJ, Walker BH. (eds.) Ecology of Tropical Savannas. Berlin/Heidelberg, Springer. Pp. 273–291.

Daibes LF, Gorgone-Barbosa E, Silveira FAO, Fidelis A. 2018. Gaps critical for the survival of exposed seeds during Cerrado fires. Australian Journal of Botany 66: 116–123. doi: 10.1071/bt17098

Daibes LF, Pausas JG, Bonani N, Nunes J, Silveira FAO, Fidelis A. 2019. Fire and legume germination in a tropical savanna: ecological and historical factors. Annals of Botany 123: 1219–1229. doi: 10.1093/aob/mcz028

Daibes LF, Zupo T, Silveira FAO, Fidelis A. 2017. A field perspective on effects of fire and temperature fluctuation on Cerrado legume seeds. Seed Science Research 27: 74–83. doi: 10.1017/s096025851700006x

D'Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23: 63–87. doi: 10.1146/annurev.es.23.110192.000431

Durigan G, Pilon NAL, Assis GB, Souza FM, Baitello JB. 2018. Plantas pequenas do Cerrado: Biodiversidade negligenciada. São Paulo, Secretaria do Meio Ambiente do Estado de São Paulo.

Escobar DFE, Silveira FAO, Morellato LPC. 2018. Timing of seed dispersal and seed dormancy in Brazilian savanna: two solutions to face seasonality. Annals of Botany 121: 1197–1209. doi: 10.1093/aob/mcy006

Fichino BS, Dombroski JRG, Pivello VR, Fidelis A. 2016. Does Fire Trigger Seed Germination in the Neotropical Savannas? Experimental Tests with Six Cerrado Species. Biotropica 48: 181-187. doi: 10.1111/btp.12276

Fidelis A, Daibes LF, Martins AR. 2016. To resist or to germinate? The effect of fire on legume seeds in Brazilian subtropical grasslands. Acta Botanica Brasilica 30: 147–151. doi: 10.1590/0102-33062015abb0187

Frenkel RE. 1977. Ruderal Vegetation Along Some California Roadsides. Berkeley, University of California Press.

Gorgone-Barbosa E, Pivello VR, Bautista S, Zupo T, Rissi MN, Fidelis A. 2015. How can an invasive grass affect fire behavior in a tropical savanna? A community and individual plant level approach. Biological Invasions 17: 423–431. doi: 10.1007/s10530-014-0740-z

Hartig F. 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.4.6. Available at: < https://CRAN.R-project.org/package=DHARMa > Accessed on 08 July 2025.

Juhász CEP, Cursi PR, Cooper M, Oliveira TC, Rodrigues RR. 2006. Dinâmica físico-hídrica de uma topossequência de solos sob savana florestada (cerradão) em Assis, SP. Revista Brasileira de Ciência do Solo 30: 401–412. doi: 10.1590/s0100-06832006000300002

Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock R.A. 2011. Fire as an evolutionary pressure shaping plant traits. Trends in Plant Science 16: 406–411. doi: 10.1016/j.tplants.2011.04.002

Kotze D. 2013. The effects of fire on wetland structure and functioning. African Journal of Aquatic Science 38: 237–247. doi: 10.2989/16085914.2013.828008

Lehmann CER, Archibald SA, Hoffmann WA, Bond WJ. 2011. Deciphering the distribution of the savanna biome. New Phytologist 191: 197–209. doi: 10.1111/j.1469-8137.2011.03689.x

Lloret F, López-Soria L. 1993. Resprouting of *Erica multiflora* after experimental fire treatments. Journal of Vegetation Science 4: 367–374. doi: 10.2307/3235595

Miranda AC, Miranda HS, de Fátima Oliveira Dias I, de Souza Dias BF. 1993. Soil and air temperatures during prescribed cerrado fires in Central Brazil. Journal of Tropical Ecololy 9: 313–320. doi: 10.1017/S0266467400007367

Moreira B, Pausas JG. 2012. Tanned or burned: the role of fire in shaping physical seed dormancy. PLoS One 7: e51523. doi: 10.1371/journal.pone.0051523

Moreira B, Tormo J, Estrelles E, Pausas JG. 2010. Disentangling the role of heat and smoke as germination cues in Mediterranean Basin flora. Annals of Botany 105: 627–635. doi: 10.1093/aob/mcq017

Ocampo-Zuleta K, Paula S, Pausas JG, Cavieres LA, Sierra-Almeida Á, Gómez-González S. 2025. Post-fire germination and plant invasion in Mediterranean Chile. American Journal of Botany 112: e70057. doi: 10.1002/ajb2.70057

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, *et al.* 2001. Terrestrial ecoregions of the world: a new map of life on Earth. BioScience 51: 933–938. doi: 10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Ooi MKJ, Denham AJ, Santana VM, Auld TD. 2014. Temperature thresholds of physically dormant seeds and plant functional response to fire: variation among species and relative impact of climate change. Ecology and Evolution 4: 656–671. doi: 10.1002/ece3.973

Paula S, Pausas JG. 2008. Burning seeds: germination response to heat treatments in relation to resprouting ability. Journal of Ecology 96: 543–552. doi: 10.1111/j.1365-2745.2008.01359.x

Pausas JG, Keeley JE. 2009. A Burning Story: The role of fire in the history of life. BioScience 59: 593–601. doi: 10.1525/bio.2009.59.7.10

Pausas JG, Keeley JE. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. New Phytologist 204: 55–65. doi: 10.1111/nph.12921

Pausas JG, Lamont BB. 2022. Fire-released seed dormancy – a global synthesis. Biological Reviews 97: 1612–1639. doi: 10.1111/brv.12855

Pilon NAL, Cava MGB, Hoffmann WA, Abreu RCR, Fidelis A, Durigan G. 2021. The diversity of post-fire regeneration strategies in the cerrado ground layer. Journal of Ecology 109: 154–166. doi: 10.1111/1365-2745.13456

Pivello VR, Martins M, Christianini AV, Carmignotto AP, Gomes BF, Fidelis A. 2025. Fire in the Cerrado. In: Fidelis A, Pivello VR. (eds.) Fire in the South American Ecosystems. Ecological Studies, vol 250. Cham, Springer. Pp. 113–155. doi: 10.1007/978-3-031-89372-8_5

Prochazka LS, Alcantara S, Rando JG, Vasconcelos T, Pizzardo RC, Nogueira A. 2024. Resource availability and disturbance frequency shape evolution of plant life forms in Neotropical habitats. New Phytologist 242: 760–773. doi: 10.1111/nph.19601

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Available at: < https://www.R-project.org/ > Accessed on 08 July 2025.

Ramos-Neto MB, Pivello VR. 2000. Lightning fires in a Brazilian savanna national park: rethinking management strategies. Environmental Management 26: 675–684. doi: 10.1007/s002670010124

Ranal MA, Santana DG. 2006. How and why to measure the germination process? Revista Brasileira de Botânica 29: 1–11. doi: 10.1590/S0100-84042006000100002

Ribeiro JWF. 2014. Aspectos do nicho de regeneração em duas espécies de *Gochnatia* (Asteraceae) em comunidade de cerrado. M.Sc. dissertation. Universidade Estadual Paulista, Brazil. Available at: < https://repositorio.unesp.br/items/4e1244c1-0718-43d9-9697-81bff5d471df > Accessed 02 June 2025.

Ribeiro JWF, Kolb RM. 2016. Distinct germination responses may contribute to the distribution pattern of two *Moquiniastrum* species in different phytophysiognomies from the Brazilian savanna. Flora 223: 159–166. doi: 10.1016/j.flora.2016.06.001

Ribeiro LC, Borghetti F. 2014. Comparative effects of desiccation, heat shock and high temperatures on seed germination of savanna and forest tree species. Austral Ecology 39: 267–278. doi: 10.1111/aec.12076

Ribeiro LC, Pedrosa M, Borghetti F. 2013. Heat shock effects on seed germination of five Brazilian savanna species. Plant Biology 15: 152–157. doi: 10.1111/j.1438-8677.2012.00604.x

Rossi RD, Martins CR, Viana PL, Rodrigues EL, Figueira JEC. 2014. Impact of invasion by molasses grass (*Melinis minutiflora* P. Beauv.) on native species and on fires in areas of campo-cerrado in Brazil. Acta Botanica Brasilica 28: 631–637. doi: 10.1590/0102-33062014abb3390

Ruprecht E, Fenesi A, Fodor EI, Kuhn T. 2013. Prescribed burning as an alternative management in grasslands of temperate Europe: The impact on seeds. Basic and Applied Ecology 14: 642–650. doi: 10.1016/j.baae.2013.09.006

Santana VM, Baeza MJ, Blanes MC. 2013. Clarifying the role of fire heat and daily temperature fluctuations as germination cues for Mediterranean Basin obligate seeders. Annals of Botany 111: 127–134. doi: 10.1093/aob/mcs238

Schmidt IB, Eloy L. 2020. Fire regime in the Brazilian savanna: recent changes, policy and management. Flora 268: 151613. doi: 10.1016/j.flora.2020.151613

Secretaria do Meio Ambiente. 2007. Plano de manejo da Floresta Estadual de Assis. Secretaria do Meio Ambiente, São Paulo. Available at: < https://smastr16.blob.core.windows.net/iflorestal/RIF/SerieRegistros/IFSR30/IFSR30.pdf >. Accessed on 22 May 2025.

Segura-Garcia C, Alencar A, Arruda VLS, Bauman D, Silva W, Conciani DE, *et al*. 2025. The fire regimes of the Cerrado and their changes through time. Philosophical Transactions of the Royal Society B 380: 20230460. doi: 10.1098/rstb.2023.0460

Tannus JLS, Assis MA, Morellato LPC. 2006. Fenologia reprodutiva em campo sujo e campo úmido numa área de Cerrado no sudeste do Brasil, Itirapina – SP. Biota Neotropica 6: bn02806032006. doi: 10.1590/S1676-06032006000300008

Vasconcelos PB, Araújo GM, Bruna EM. 2014. The role of roadsides in conserving Cerrado plant diversity. Biodiversity and Conservation 23: 3035–3050. doi: 10.1007/s10531-014-0762-y

Vaz AMSF, Santos ACB. 2025. *Bauhinia* in Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro. Available at: < https://floradobrasil.jbrj.gov.br/FB111840>. Accessed on 21 May 2025.

Williams PR, Congdon RA, Grice AC, Clarke PJ. 2003. Fire-related cues break seed dormancy of six legumes of tropical eucalypt savannas in north-eastern Australia. Austral Ecology 28: 507–514. doi: 10.1046/j.1442-9993.2003.01307.x

Zirondi HL, Silveira FAO, Fidelis A. 2019. Fire effects on seed germination: Heat shock and smoke on permeable vs impermeable seed coats. Flora 253: 98–106. doi: 10.1016/j.flora.2019.03.007

Zupo T, Baeza MJ, Fidelis A. 2016. The effect of simulated heat-shock and daily temperature fluctuations on seed germination of four species from fire-prone ecosystems. Acta Botanica Brasilica 30: 514–519. doi: 10.1590/0102-33062016abb0246

Zupo T, Daibes LF, Pausas JG, Fidelis A. 2021. Post-fire regeneration strategies in a frequently burned Cerrado community. Journal of Vegetation Science 32: e12968. doi: 10.1111/jvs.12968

Zupo T, Gorgone-Barbosa E, Rissi MN, Daibes LF. 2022. Experimental burns in an open savanna: greater fuel loads result in hotter fires. Austral Ecology 47: 1101–1112. doi: 10.1111/aec.13202