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Post-fire regeneration strategies in a frequently burned Cerrado community

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Abstract

Aim: Fire is a natural disturbance in many ecosystems throughout the world where plant populations can persist by the resprouting of individuals and/or by recruiting from seeds. We evaluated the post-fire regeneration response for 41 coexisting species, including grasses, forbs, and shrubs, from an open Cerrado community (*campo sujo*) in Central Brazil.

Location: The study was conducted at the Reserva Natural Serra do Tombador (RNST) in Central Brazil. The vegetation of the study area is characterized by a continuous herbaceous layer dominated by grasses and scattered shrubs, which produces fine fuel loads that can burn frequently.

Methods: We examined both resprouting ability after experimental fires, accounting for bud location, and seed response to heat shocks caused by fire, where seeds were subjected to heat shocks of 100°C for one and three minutes, 200°C for one minute, and a control (untreated seeds).

Results: All species were able to resprout (R+) after fire, mainly from buds located in underground structures, but also from aerial and basal buds. Seeds of most species tolerated heat shocks of 100°C for one and three minutes, but heat treatments of 200°C decreased seed viability of nearly 50% of species. Seven species, all of which had dormant seeds, showed heat-stimulated germination. In sum, 81% of the community was classified as R+PT (resprouters with heat-tolerant propagules) and 17% was R+PS (resprouters with heat-stimulated propagules). The remaining 2% (one species) was classified as R+P−, showing heat-sensitive seeds.

Conclusions: Resprouting is the main post-fire regeneration strategy in Cerrado open savannas, while fire-stimulated germination, although possible, is less common in comparison to the frequency in other fire-prone ecosystems. However, in Cerrado open savannas, heat tolerance is an important trait that enables germination when favorable conditions arise.

KEYWORDS
germination, heat shocks, Neotropical savanna, post-fire resprouting, post-fire seeding

1 | INTRODUCTION

Fire is a main disturbance in many ecosystems worldwide (Bond & van Wilgen, 1996; Bond & Keeley, 2005). Both resprouting from protected buds and recruitment from seeds have been recognized as key regeneration traits; species may have one of these traits, both, or none (Pausas et al., 2004; Vesk et al., 2004; Paula & Pausas, 2008). Thus, classification for regeneration strategies in fire-prone ecosystems is usually based on whether individuals are killed or survive a fire episode by resprouting (Bond & Midgley, 2001, 2003; Clarke et al., 2015), and/or whether plant species can form a fire-resistant seed bank, usually showing fire-stimulated germination (Pausas et al., 2004; Pausas & Keeley, 2014).

Such mechanisms of post-fire regeneration are favored or limited by both environmental conditions, site productivity and resource availability, and fire regimes at a given site, which includes fire frequency, intensity, season and patterns of fuel consumption (Bond & Midgley, 2003; Bond & Keeley, 2005; Clarke et al., 2005; Keeley et al., 2012; Pausas & Ribeiro, 2013). Different fire regimes select different functional traits; thus, plant species are adapted to a specific fire regime rather than to fire itself (Pausas & Keeley, 2009; Keeley et al., 2011).

These two mechanisms have been described and mostly studied in Mediterranean-type vegetation, where fires consume most canopy biomass of woody plants (crown fires), are considered of high intensity and occur at intervals of several decades (Keeley et al., 2011; Keeley et al., 2012; Pausas & Keeley, 2014). In such systems, high temperatures and prolonged soil heating could affect resprouting responses by damaging buds or bud-forming tissues (Vesk et al., 2004; Wright & Clarke, 2007) and recruitment from seeds would be frequent (Bond & Midgley, 2003; Pausas & Keeley, 2014; Clarke et al., 2015). In Australian crown-fire systems, around 40% of species display both post-fire resprouting and post-fire seeding, and up to 57% of species are obligate seeders, regenerating exclusively from seeds after fires (Pausas et al., 2004; Clarke et al., 2015).

In contrast, open ecosystems such as savannas and grasslands undergo surface fires, which have a relatively low intensity, fast rates of spread (rapidly consuming the grassy layer), and can reoccur within intervals of a few years (Miranda et al., 2002; Bond & Keeley, 2005; Archibald et al., 2013; Pausas & Ribeiro, 2013). Under such regimes, the most likely fire response would be resprouting as short fire intervals would prevent seedlings and saplings of reaching maturity (Bellingham & Sparrow, 2000; Bond & Midgley, 2001, 2003; Pausas & Keeley, 2014). Location, protection, and number of buds are main drivers of post-fire resprouting and adult individuals can resprout from aerial, basal or below-ground buds, given that the meristematic tissues survive the high temperatures caused by fire (Clarke et al., 2013; Clarke et al., 2015; Charles-Dominique et al., 2015; Pausas et al., 2018; Pausas & Paula, 2020).

Fire-related seeding is often associated with synchronizing germination to a single point in time, where germination may be triggered by different fire cues, such as heat shocks (Auld & Denham, 2006; Reyes & Trabaud, 2009; Moreira et al., 2010; Moreira & Pausas, 2012), temperature fluctuations (Santana et al., 2010; Musso et al., 2015; Daibes et al., 2017; Dairel & Fidelis, 2020), and smoke (Keeley & Fotheringham, 2000; Keeley & Pausas, 2018; Zirondi, José, et al., 2019). Heat shocks caused by fire have been reported to stimulate germination in several species of fire-prone ecosystems, such as those in Australia and in the Mediterranean region, mainly in hard-seeded species in which high temperatures may break physical dormancy, thus enabling germination (Auld & O'Connell, 1991; Williams et al., 2003; Reyes & Trabaud, 2009; Moreira et al., 2010; Moreira & Pausas, 2012). Nonetheless, heat shocks have shown little to no effect among species of South America, although most seeds were able to survive the exposure to high temperatures, which is considered a tolerance trait in face of fires (Jaureguiberry & Diaz, 2015; Le Stradic et al., 2015; Ribeiro et al., 2015; Fichino et al., 2016; Fidelis et al., 2016; Zupo et al., 2016; Gómez-González et al., 2017; Daibes et al., 2019; Zirondi, José, et al., 2019).

In the Cerrado, frequent fires have been present for at least four million years (Simon et al., 2009) and fire regimes are characterized by frequent (~3 to 5 years) surface fires of relatively low intensity fueled by grasses (Coutinho, 1982; Kauffman et al., 1994; Miranda et al., 2002, 2009; Pereira-Junior et al., 2014; Alvarado et al., 2017; Rissi et al., 2017). After fires, many woody and herbaceous species resprout from dormant buds (Coutinho, 1990; Medeiros & Miranda, 2008; Pausas et al., 2018; Pilon et al., 2020), but the role of post-fire seed germination as a regeneration mechanism in Cerrado remains unclear. Even though post-fire seed germination has been observed in grasslands and savannas that undergo surface fires (Overbeck & Pfadenhauer, 2007; Clarke et al., 2015; Ramos et al., 2019; Pilon et al., 2020), studies evaluating seed responses after heat shocks in the Cerrado have done so with few species (Ribeiro et al., 2013; Le Stradic et al., 2015; Fichino et al., 2016) or are restricted to certain clades (Ramos et al., 2016; Daibes et al., 2019; Zirondi, José, et al., 2019; Dairel & Fidelis, 2020), hindering the understanding of general post-fire regeneration mechanisms at the community scale. Moreover, few studies addressing fire-related seed responses in the Cerrado have taken into account plant resprouting ability following experimental fires (but see Pilon et al., 2020).

In this context, we aimed to investigate the role of both post-fire resprouting and fire-related seeding as regeneration strategies for 41 coexisting species, including shrubs, forbs, and grasses from a frequently burned Cerrado community (open savanna). We assessed: (a) resprouting ability after experimental fires, accounting for bud location; and (b) propagule stimulation and/or tolerance to heat shocks by evaluating seed germination and viability after laboratory trials. Since fire regime is expected to shape post-fire regeneration strategies (Bond & Midgley, 2003; Keeley et al., 2012), we expect resprouting to be the main regeneration strategy in the Cerrado (Bond & Midgley, 2001; Clarke et al., 2015; Pilon et al., 2020) with heat shocks having little effect on seed germination (Le Stradic et al., 2015; Fichino et al., 2016; Ramos et al., 2016; Ramos et al., 2019;

Zirondi, José et al., 2019). We also expect propagules to be tolerant to fire-related temperatures (Daibes et al., 2019), remaining ungerminated (yet viable) until the onset of the rainy season (Escobar et al., 2018).

2 | METHODS

2.1 | Study area and seed collection

The study was conducted at the Reserva Natural Serra do Tombador (RNST) in Central Brazil (47°45′–47°51′ W and 13°35′–13°38′ S, 8,900 ha, 560–1,118 m a.s.l). The vegetation of the study area, characterized as Cerrado *campo sujo*, is an open-savanna vegetation with a continuous herbaceous layer dominated by grasses and scattered shrubs (Coutinho, 1978). The climate is defined by a marked dry season from May to September (total precipitation during this period is <60 mm) and a wet season from October to April, when most of the annual precipitation is concentrated (1,300–1,500 mm/year). Minimum temperatures may be lower than 15°C and maximum temperatures can reach up to 36°C (Fundação Grupo Boticário, 2011). The RNST has been subjected to natural and anthropogenic fires, especially in grassland and savanna sites, with a mean fire return interval of three years (Daldegan et al., 2014).

Seeds from 41 coexisting open-savanna species, including different growth forms (grasses, forbs, and shrubs), were used in this study (Table 1). Germination data for 26 of the 41 species are original to this study (Appendix S1); for the remaining species, we compiled data from Daibes et al. (2019); Zirondi, José et al., 2019 and Zirondi, Silveira et al. (2019), which used the same treatments (see *Methods* below) with species collected in the same area (Table 1). All seeds were collected throughout different seasons of the year between 2014 and 2016 (Appendix S2; Daibes et al., 2019; Zirondi, José et al., 2019 and Zirondi, Silveira et al. 2019) from the most representative families in the area, mainly Fabaceae (15 species), Asteraceae (four species), Lamiaceae (four species), and Poaceae (four species). Seeds of most species were collected from several individuals (n > 10), except for *Dyckia brasiliana* where seeds were collected from three individuals. Seeds were stored at low temperatures (<20°C) prior to the experiments; experiments were usually set up one to two months after seeds were harvested.

2.2 | Resprouting ability

We addressed resprouting ability for the same species from which we collected seeds. We observed individuals (at least five individuals per species) in the field after fires. From 2012 to 2016, two prescribed fire experiments have been set up in the RNST (see Gorgone-Barbosa et al., 2015; Rissi et al., 2017) where several plots were burned throughout the years. In addition, in 2015 and 2016 an extensive area next to one of the areas where the experimental plots were set up was also burned as a long fire break was carried out by the reserve's fire brigade. From 2012 to 2016, these areas have been monitored every three months, where we observed conspicuous post-fire resprouting of the species used in this study (as they are abundant within the experimental plots and in the adjacent areas); and, whenever possible, we determined the location from where the resprouting shoots were originating: underground, aerial or basal buds (Clarke et al., 2013). Underground buds refer to buds located in specialized underground structures (i.e., xylopodium, bulbs, and rhizomes), basal buds refer to buds located in the root-crown, and aerial buds refer to epicormic or apical buds.

2.3 | Propagule germination and survival

Germination experiments were carried out to evaluate seed response to heat shocks simulating fire passage. Seeds of all species were sorted prior to the germination trials to avoid empty seeds. Seeds were then subjected to four different treatments prior to germination tests: (a) heat treatment of 100°C for 1 min; (b) heat treatment of 100°C for 3 min; (c) heat treatment of 200°C for 1 min; and (d) control (untreated seeds). This combination of temperature and time was determined from previous studies that observed heat pulses on the soil surface and in the soil seed bank (1 cm below-ground) for Cerrado open savannas (Miranda et al., 1993; Daibes et al., 2017, 2018). For each species, we used five replicates containing 20 seeds in each treatment (n = 100 seeds/treatment). Treatments were applied separately for each replicate in an electric oven to ensure independence of data (Morrison & Morris, 2000). Seeds of *Vellozia* spp., *Xyris* sp., *Dyckia brasiliana*, *Mimosa pteridifolia*, and *Senna corifolia* were not subjected to the treatment at 100°C for 3 min due to a limited number of available seeds (Daibes et al., 2019; Zirondi, José et al., 2019; Zirondi, Silveira et al. 2019).

After treatments, seeds were placed in Petri dishes with two layers of filter paper saturated with distilled water, and put in germination chambers at 27°C (12 hr of light). Seed germination was recorded three times a week during 30 days and germination was determined by radicle emergence (Bewley et al., 2013). Physiological dormancy (PD) was assigned for species that had less than 30% germination of the number of viable seeds in the control treatment, during the 30 days of the tests (Baskin & Baskin, 2014; Dayrell et al., 2017). Species that had a germination percentage between 30% and 70% of the number of viable seeds were assigned to have "intermediate" dormancy, while those with >70% germination were considered non-dormant (see also Dayrell et al., 2017). Species with hard-coated seeds that showed no visible signs of imbibition by the end of the tests in the control were assigned as physically dormant (PY). In such cases, seeds were then manually scarified with a sandpaper and allowed to imbibe and germinate for one week. Within this period, the germinated seeds were counted as viable, and thus we also assured they had no combined physiological dormancy.

TABLE 1 Family, species, growth form, initial viability, dormancy class or non-dormancy (PY = physical dormancy, PD = physiological dormancy, MPD = morphophysiological dormancy, ND = non-dormant), bud location (aerial, basal, underground), and classification of regeneration strategy according to resprouting and seed germination responses to heat: R+PT = resprouter and heat-tolerant propagules; R+PS = resprouter and heat-stimulated propagules; R+P− = resprouter and heat-sensitive propagules

Family	Species	Growth form	Initial viability (%)	Dormancy	Bud location	Regeneration strategy
Asteraceae	*Aldama grandiflora* (Gardner) E.E.Schill. & Panero	Forb	56	ND	Underground	R+PT
	Lessingianthus buddlejifolius (Mart. ex DC.) H.Rob.	Shrub	30	ND	Underground	R+PT
	Lessingianthus floccosus (Gardner) H Rob.	Shrub	26	ND	Underground	R+PT
	Lessingianthus hoveaefolius (Gardner) H.Rob.	Shrub	13	ND	Underground	R+PT
Bromeliaceae	*Dyckia brasiliana* L.B.Sm.	Forb	68	ND	Basal	R+PT
Calophyllaceae	*Kielmeyera rubriflora* Cambess.	Shrub	29	ND	Underground	R+PT
Cyperaceae	*Bulbostylis paradoxa* (Spreng.) Lindm.	Graminoid	84	ND	Aerial	R+PT
Dilleniaceae	*Davilla elliptica* A.St.-Hi.	Shrub	85	MPD*	Aerial	R+PT
Fabaceae	*Bauhinia dumosa*[3] Benth.	Shrub	98	ND	Underground	R+PT
	Chamaecrista claussenii (Benth.) H.S.Irwin & Barneby	Shrub	66	PY	Underground	R+PT
	Chamaecrista ochrosperma[1] (H.S.Irwin & Barneby) H.S.Irwin & Barneby	Shrub	84	PY	Underground	R+PT
	Harpalyce tombadorensis São-Mateus et al.	Shrub	51	PY	Underground	R+PT
	Mimosa claussenii[1] Benth.	Shrub	80	PY	Aerial	R+PT
	Mimosa kalunga[1] Marc.F.Simon & C.E.Hughes	Shrub	48	PY	Underground/ aerial	R+PS
	Mimosa leiocephala[3] Benth.	Shrub	74	PY	Underground	R+PS
	Mimosa pteridifolia[3] Benth.	Shrub	60	ND	Underground	R+P−
	Mimosa gracilis Benth.	Forb	47	ND	Underground	R+PT
	Mimosa[1] sp1	Shrub	91	PY	Aerial	R+PT
	Mimosa[1] sp2	Shrub/Tree	100	ND	Aerial	R+PT
	Senna cana[1] (Nees & Mart.) H.S.Irwin & Barneby	Shrub/Tree	90	PY	Undetermined	R+PS
	Senna corifolia[1] (Benth.) H.S. Irwin & Barneby	Shrub	81	PY	Underground	R+PT
	Senna silvestris[1] (Vell.) H.S. Irwin & Barneby	Shrub/Tree	84	PY (intermediate)	Undetermined	R+PT
	Stylosanthes sp.	Shrub	100	PY (intermediate)	Underground	R+PS
Gentianaceae	*Deianira pallescens* Cham. & Schltdl.	Forb	81	ND	Underground	R+PT
Iridaceae	*Trimezia juncifolia* (Klatt) Benth. & Hook.f.	Forb	73	ND	Underground	R+PT
Lamiaceae	*Cyanocephalus coriaceus* (Benth.) Harley & J.F.B.Pastore	Forb	82	ND	Underground	R+PT
	Hypenia brachystachys (Pohl ex Benth.) Harley	Forb	22	ND	Underground	R+PT
	Hypenia sp.	Forb	71	ND	Underground	R+PT
	Medusantha mollissima (Benth.) Harley & J.F.B.Pastore.	Shrub	66	ND	Underground	R+PT
Lythraceae	*Diplusodon punctatus* Pohl	Shrub	53	PD	Underground	R+PS
Malvaceae	*Melochia* sp.	Shrub	86	PY	Underground	R+PS

(Continues)

TABLE 1 (Continued)

Family	Species	Growth form	Initial viability (%)	Dormancy	Bud location	Regeneration strategy
Melastomataceae	*Tibouchina melastomoides*[3] (Naudin) Cogn.	Forb	44	ND	Underground	R+PT
Poaceae	*Elionurus muticus* (Spreng.) Kuntze	Graminoid	88	ND	Basal	R+PT
	Aristida riparia Trin.	Graminoid	35	PD	Basal	R+PT
	Aristida setifolia Kunth	Graminoid	42	PD	Basal	R+PS
	Axonopus aureus P.Beauv.	Graminoid	72	ND	Underground	R+PT
Velloziaceae	*Vellozia glochidea*[2] Pohl	Shrub	99	ND	Aerial	R+PT
	Vellozia squamata[2] Pohl	Shrub	57	ND	Aerial	R+PT
	Vellozia tubiflora[2] (A.Rich.) Kunth	Shrub	48	ND	Aerial	R+PT
Verbenaceae	*Lippia lupulina* Cham.	Shrub	25	ND	Underground	R+PT
Xyridaceae	*Xyris* sp.	Forb	81	ND	Basal	R+PT

[1] Experimental data from Daibes et al., (2019).

[2] Experimental data from Zirondi, José, et al., (2019).

[3] Experimental data from Zirondi, Silveira, et al. (2019).

*Type of dormancy inferred from information on germination and on seed characteristics of the family.

Viability of non-germinated seeds of the visibly imbibed soft-coated seeds was analyzed at the end of each experiment by means of the Tetrazolium test at 1% solution. Those staining red were considered viable, those not stained or showing flaccid tissues were considered dead (Lakon, 1949). The average of viable seeds (germinated + stained) from control replicates was used as the initial viability.

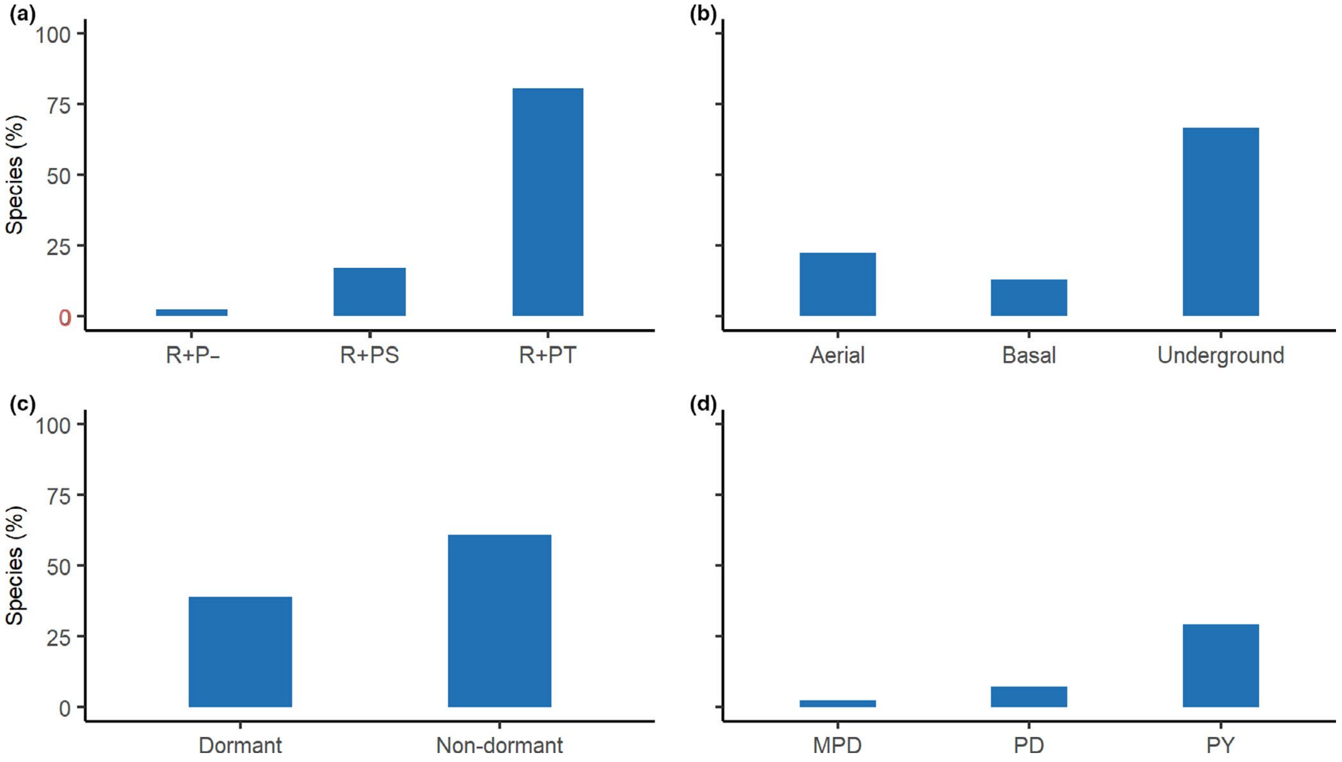


FIGURE 1 Percentage of species in the community that were: (a) classified as R+PT (resprouter and heat-tolerant propagules), R+PS (resprouter and heat-stimulated propagules), and R+P− (resprouter and heat-sensitive propagules); (b) observed with resprouts originating from underground, basal, and aerial buds; (c) classified as dormant and non-dormant; and (d) classified in each of the following dormancy classes: physical dormancy (PY), physiological dormancy (PD), and morpho-physiological dormancy (MPD)

2.4 | Classification of post-fire strategies

Regarding resprouting ability, the species used in this study were classified as R+, species that were able to resprout after fires, or R−, species that were not able to resprout but were killed by fires (Pausas et al., 2004). Regarding the germination response to heat treatments, we defined three types of responses based on Paula and Pausas (2008) and Jaureguiberry and Díaz (2015): (a) heat-tolerant propagules (PT), germination or viability after at least one of the heat treatments equal to that after the control treatment; (b) heat-stimulated propagules (PS), germination after at least one of the heat treatments higher than that after the control treatment; and (c) heat-sensitive propagules (P−), germination or viability after all heat treatments significantly lower than that after the control treatment.

2.5 | Data analysis

One-way analysis of variance applied to randomization tests (Euclidean distance between sampling units, 10,000 iterations) were carried out to evaluate differences in percentage of germination and viability between the different treatments (fixed factor) for each species; these analyses were performed using MULTIV (Pillar, 2008). We tested if post-fire regeneration strategy was associated with bud location, dormancy or growth form with χ^2 tests, which were carried out in R software (R Core Development Team 2016).

3 | RESULTS

All species were able to resprout (R+) after fire, mainly from buds located in underground structures (26 species, 67%), but also from aerial (9 species, 23%) and basal (5 species, 13%) buds; we did not observe non-resprouting (R−) species (Table 1, Figure 1a,b). Most species (81%) had propagules which resisted at least one of the heat treatments, and were thus classified as heat-tolerant (PT). Seven species (17%) had enhanced germination after at least one of the heat shock treatments and were classified as heat-stimulated (PS) and only one species (*Mimosa pteridifolia*) showed heat-sensitive propagules (P−; Table 1, Figure 1a), with decreased germination and viability in all heat treatments compared to the control. Thus, regarding post-fire regeneration strategies, 81% of the community's species were classified as R+PT (resprouters with heat-tolerant propagules), 17% as R+PS (resprouters with heat-stimulated propagules), and 2% as R+P− (resprouter with heat-sensitive propagules; Table 1, Figure 1a). Moreover, 25 species (61%) had non-dormant seeds and 16 species (39%) had dormant seeds (Figure 1c), of which two species were classified with intermediate dormancy (Table 1). Among dormant species, twelve species (75%) had physical dormancy (PY), three species (19%) had physiological dormancy (PD), and only one had morphophysiological dormancy (MPD, Figure 1d).

TABLE 2 Pearson residuals of the chi-square (χ^2) test between regeneration strategy and bud location, dormancy, and growth forms for 41 Cerrado species from central Brazil

	R+P−	R+PS	R+PT
Bud location			
Aerial	−0.474	−0.458	0.298
Basal	−0.353	0.133	0.00
Underground	0.434	0.211	−0.175
Dormancy			
Dormant	−0.624	2.582	−1.081
Non-dormant	0.499	−2.065	0.864
Growth form			
Forb	−0.487	−1.093	0.575
Graminoid	−0.345	−0.024	0.077
Shrub	0.445	0.818	−0.481

Post-fire regeneration strategy showed no association with bud location ($\chi^2 = 0.93$, $P = 0.9$), where species with heat-stimulated propagules were evenly distributed among underground, basal and aerial resprouters (Table 2, Figure 2a). However, there was a strong association between post-fire regeneration strategy and seed dormancy ($\chi^2 = 14.83$, $P < 0.001$), where all species that had heat-stimulated propagules (R+PS) had dormant seeds (Table 2, Figure 2b). In addition, although heat-stimulated propagules tended to be negatively associated to forbs (Table 2, Figure 2c), we found no relationship between post-fire regeneration strategy and growth forms ($\chi^2 = 3.95$, $P = 0.42$).

Most species survived exposure to 100°C for one and three minutes, but nearly 50% of species showed decreased viability when exposed to 200°C (Figure 3). Moreover, germination of nearly 30% of species also decreased when exposed to 200°C, while for six species, even though seed viability decreased when exposed to 200°C, seed germination was not affected. For species that showed heat-stimulated propagules, heat treatments of 100°C for three minutes and 200°C were equally effective in stimulating germination, except for *Mimosa kalunga* (PS only with 100°C for three minutes) and *Aristida setifolia* (PS only with 200°C). Interestingly, although 200°C stimulated seed germination for *Stylosanthes* sp. and *Melochia* sp., it also decreased seed viability (Appendix S1).

4 | DISCUSSION

All species were able to resprout after fire (R+), indicating that, as expected, resprouting is the main post-fire regeneration strategy in the Cerrado open savannas. Although non-resprouters have been found in fire-prone ecosystems subjected to surface fires, including the Australian savannas (Clark et al., 2015) and a Cerrado open savanna from southeast Brazil (Pilon et al., 2020), it plays a minor role in these ecosystems, representing only 7%–10% of the flora. Nonetheless, our frequently burned Cerrado community lacked non-resprouters. Our results show that 17% could display

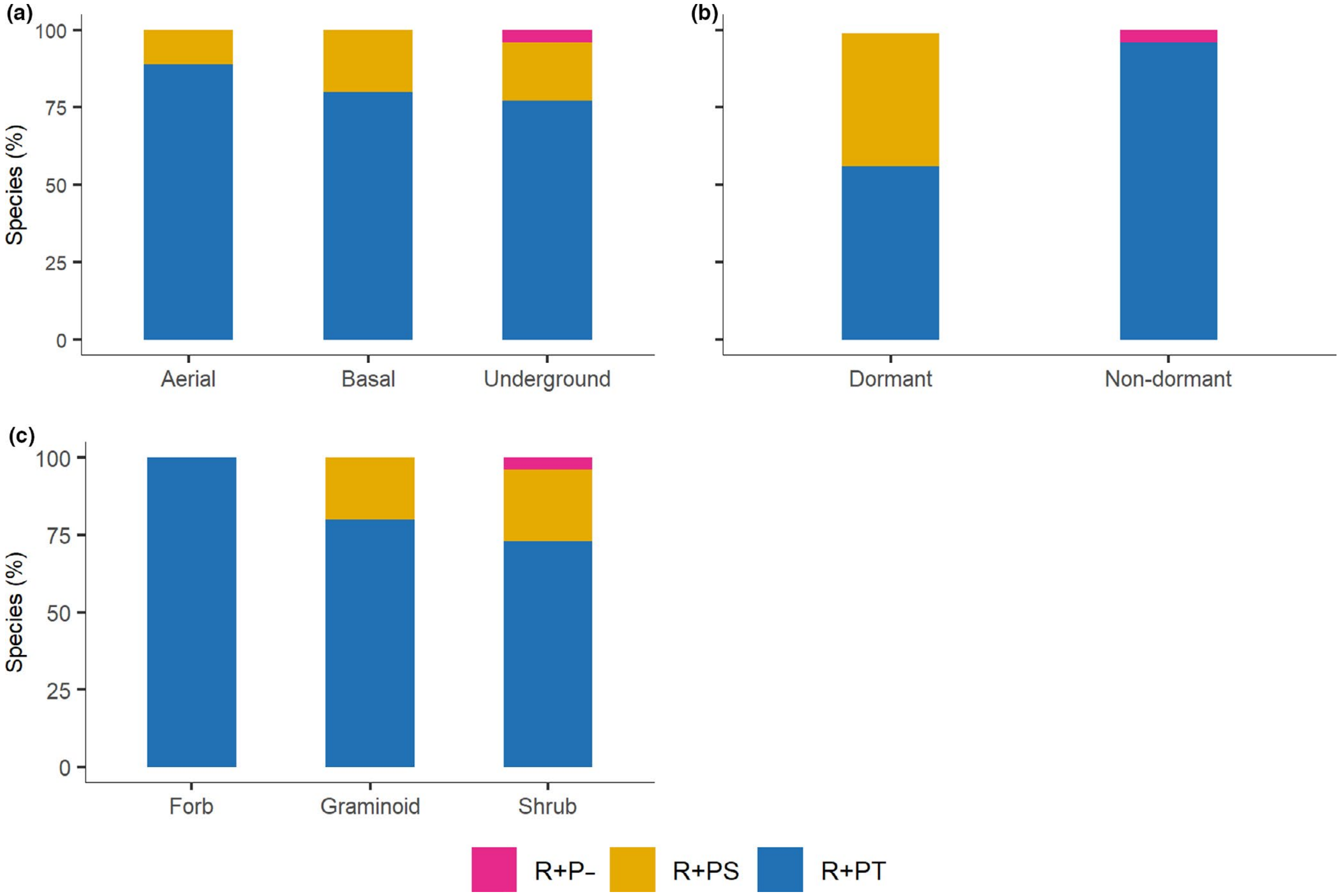
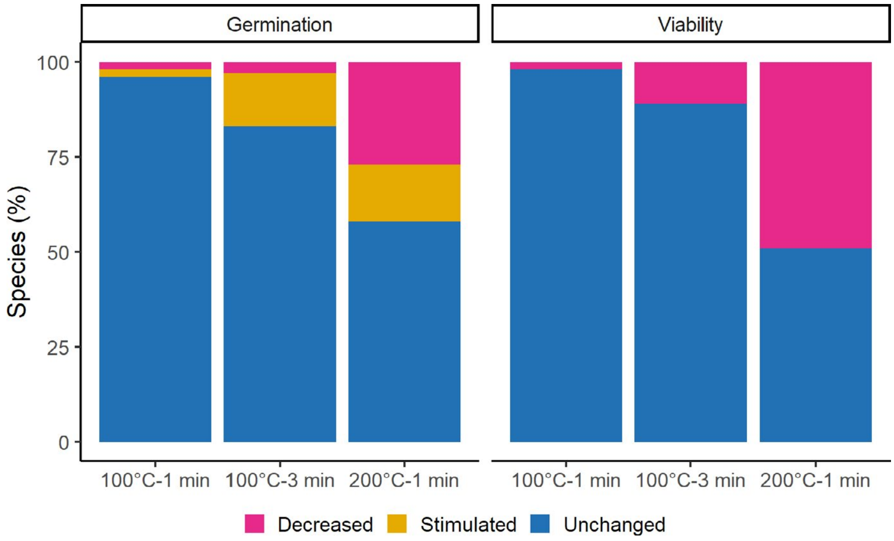


FIGURE 2 Percentage of species that were classified as R+PT (resprouter and heat-tolerant propagules), R+PS (resprouter and heat-stimulated propagules), and R+P− (resprouter and heat-sensitive propagules) in relation to: (a) bud location (resprouts originating from underground, aerial, and basal buds); (b) seed dormancy (species with dormant or non-dormant seeds); and (c) growth form

FIGURE 3 Percentage of species in the community that had its germination and viability decreased, stimulated or unchanged by heat shocks of 100°C for 1 min, 100°C for 3 min and 200°C for 1 min. Species with unchanged germination or viability (in relation to their control) were considered tolerant species (see *Methods*)



heat-stimulated germination, yet always combined with resprouting ability (R+PS; seven species), while the vast majority of species had heat-tolerant propagules but were not stimulated (R+PT; 33 species). Hence, 98% of Cerrado species are resprouters associated to some fire-related seed trait (R+PT and R+PS) that could ultimately enable germination under favorable conditions.

Climate and productivity have been suggested to interact, affecting fire regimes, especially fire frequencies (Pausas & Bradstock, 2007; Pausas & Ribeiro, 2013). Although the Cerrado is known to have nutrient-poor soils (Ratter et al., 1997), its climate is typical of the moister savanna regions of the world, with an average annual precipitation reaching up to 2,000 mm (Ratter et al., 1997) and a mean productivity around 700 g m^{-2} two years after fire (Rissi et al., 2017). Such high productivity leads to higher fire frequencies because time needed to reach critical fuel loads is reduced (Pausas & Ribeiro, 2013; Wuest et al., 2016). Thus, in environments with high disturbance frequencies, such as the Cerrado (Pereira-Júnior et al., 2014; Alvarado et al., 2017), resprouting species would be favored as their growth responses are almost immediate, and plants that quickly reoccupy gaps show a competitive advantage (Lamont et al., 2011; Clarke et al., 2013). Additionally, frequent disturbances may also favor resprouting because short fire intervals would inhibit seedling recruitment to maturity (Bellingham & Sparrow, 2000; Bond & Midgley, 2003).

Alternatively, sites with slow post-fire regeneration and large and long-lasting post-fire gaps, where competition for resources is reduced, will select for seedling recruitment over resprouting (Keeley et al., 2016). This could explain the lack of obligate seeding species and the low number of species that could potentially show heat-stimulated germination in our community. However, small bare soil gaps have been shown to influence seed germination due to enhanced daily temperature fluctuations in Cerrado open savannas (Daibes et al., 2017; Dairel & Fidelis, 2020); thus indirect environmental cues of the post-fire environment rather than heat shocks could influence recruitment from seed.

Furthermore, post-fire seeding is associated with the acquisition of a fire-resistant seed bank and delaying germination to a single point in time (i.e., after fires) when more resources are available (Pausas & Keeley, 2014). Seed dormancy, especially physical dormancy, can thus be considered a key trait in fire-prone ecosystems as it can be related to post-fire recruitment (Keeley et al., 2011; Ooi et al., 2014; He et al., 2019). Although all species that had heat-stimulated propagules in our community had dormant seeds, mostly legumes (physical dormancy), the total percentage of dormant species (around 40%) is relatively low compared to the expected percentage for savanna communities (ca. 70%, Baskin & Baskin, 2014), but similar to what has been found for other Cerrado vegetation types (Dayrell et al., 2017; Escobar et al., 2018). Moreover, less than half of the dormant species showed heat-stimulated propagules, which might indicate that the presence of fire-cued dormancy in this system is less important than for the Mediterranean-type ecosystems (Moreira & Pausas, 2012; Ooi et al., 2014; Pausas & Keeley, 2014); in many Cerrado species, seed dormancy seems to be determined by their ancestry (Dayrell et al., 2017; Daibes et al., 2019) or by seasonality (Escobar et al., 2018).

Additionally, most Cerrado species only form transient seed banks (Velten & Garcia, 2007; Salazar et al., 2011) and recruitment from the seed bank does not seem to be linked to fire, but rather to the onset of the rainy season (Andrade & Miranda, 2014; Escobar & Cardoso, 2015). Nonetheless, all species (except for *Mimosa pteridifolia*) survived one-minute heat shocks of 100°C and most survived 3-min heat shocks of 100°C, suggesting seed tolerance to these temperatures (R+PT), corroborating what has been observed for species of other fire-prone grassy ecosystems (Gashaw & Michelsen, 2002; Clarke & French, 2005; Dayamba et al., 2008), including the Cerrado (Le Stradic et al., 2015; Fichino et al., 2016; Ramos et al., 2016; Daibes et al., 2019; Zirondi, José et al., 2019). During Cerrado fires, temperatures 1 cm below-ground rarely increase over 80°C (Daibes et al., 2017), and thus fire tolerance could be an important seed trait as seeds that are occasionally stored in the soil seed bank would survive a fire episode and recruit in the following rainy season.

However, seeds of nearly 50% of species showed lower viability (and consequently lower germination for ~30% of species) when exposed to 200°C for one minute. This is a very high temperature that has not been observed below-ground (in the soil seed bank; Daibes et al., 2017, Zupo *et al*. upubl.). Thus, only recently dispersed seeds that have not been incorporated into the soil seed bank at the time of fire are likely to be killed (Daibes et al., 2017), as only temperatures on the soil surface exceed 200°C (Pivello et al., 2010; Gorgone-Barbosa et al., 2015; Daibes et al., 2017, 2018). In fact, it is more likely that seedling establishment of resprouting species occurs in the intervals between fires (Pausas & Keeley, 2014), in which the ability of juveniles to resprout would be essential for successful establishment, especially in frequently disturbed ecosystems.

On the other hand, resprouting occurred mostly from underground buds that are highly protected as they are insulated by soil (Choczynska & Johnson, 2009; Clarke et al., 2013), and that are usually found on specialized structures, such as xylopodia and underground stems, constituting the geoxyle growth form. Such a growth form is present in both the Cerrado (Simon et al., 2009; Simon & Pennington, 2012; Pausas et al., 2018) and the African savannas (Maurin et al., 2014), where it has been considered advantageous as these are areas of high precipitation and frequent fires (Maurin et al., 2014).

Furthermore, around 25% of non-dormant species had low germination and viability percentages under control conditions, mainly due to a great amount of embryo-less seeds (data not shown), as has been observed for other Cerrado communities (Le Stradic et al., 2015; Dairel & Fidelis, 2020; Dayrell et al., 2017). Lamont et al. (2011) argue that low fecundity among resprouting species may be due to accumulation of deleterious somatic mutations, given that resprouters live through many fire cycles and accumulation of mutant alleles and chromosomal aberration is a time-dependent process. Thus, low seed sets may be an inevitable consequence of the longevity of resprouters. However, resprouting can enhance fitness where fire intervals are short and seedling recruitment is limited, given that resprouters can produce seeds more quickly after fire events (Lamont et al., 2011; Keeley et al., 2011; Pausas & Keeley, 2014). Thus, perhaps the ultimate role of seeds, given that resprouting is the main post-fire regeneration mechanism, would be dispersal and the colonization of new areas.

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DATA AVAILABILITY STATEMENT

The data and source codes used are stored at https://github.com/talitazupo/seeds.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Seed germination and seed viability (%, mean ± *SE*) of 26 species after being exposed to heat shocks of 100°C – 1', 100°C – 3', 200°C – 1'.

Appendix S2. Seed collection date and season for 26 species used in this study.

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