To protect or to hide: Why not both? An investigation of fire-related strategies in Cerrado woody species

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Abstract

Two key strategies enable woody species persistence and survival in fire-prone ecosystems after fire: the aboveground protection of stems and buds by thick bark and the allocation of biomass belowground to specialized bud bearing storage organs – both strategies allowing plants to resprout new branches after the aboveground parts are damaged by fire. Here we investigate whether those two strategies can be combined with each other. We compared 24 woody species from the Cerrado (tropical savannas from Brazil) and analyzed their underground storage organs (USOs) in relation to their aboveground bark production and aerial bud protection – two key traits allowing species to first survive and then persist after fire – together with plant potential height. We then compared if bark growth rate, aerial bud protection and plant potential height are linked to the ecological function of the underground storage organs (on spot persistence vs clonal growth through lateral spreading). Species with woody rhizomes (capable of spreading laterally) better protected their aboveground stems with thicker bark when compared to species with xylopodium and root-crown organs (adapted for on spot basal resprouting). A clear division was found concerning how well species are protecting their aerial buds and the type of underground storage organ, with species spreading laterally displaying a greater aerial bud protection. The results suggest that the presence of a specialized organ belowground does not appear to be mutually exclusive with producing thick bark on aboveground stems. It does exist, however, a different expression of bark production and aerial bud protection between species displaying lateral spread and those persisting on spot, suggesting the existence of a trade-off between above- and belowground strategies in species displaying on spot persistence. This highlights that Cerrado species can combine different fire-survival strategies, further

questioning which fire conditions promote each strategy and their combination and in which cases trade-offs occur.

Keywords: Belowground organs, bark production, bark thickness, clonal growth, resprouting, underground storage organs.

1. Introduction

Species persistence in fire-prone ecosystems is highly dependent on their ability to survive fire. During a fire event, not all parts of the plants are equally exposed to the flames, with different traits being required to promote fire-survival (Chiminazzo et al., 2021; Scalon et al., 2020; Wigley et al., 2020). This is the consequence of the distribution of aboveground structures that are exposed or not to the flames: higher structures such as branches and twigs can be positioned outside the flames and are only exposed to the flame plume. On the other end, older parts of the trunk and/or main stems are located closer to the ground and are thus exposed to flames (Chiminazzo et al., 2021; Dantas and Pausas, 2013; Gignoux et al., 1997; Graves et al., 2014). Plant structures can be positioned belowground and be well insulated by the soil, where they barely suffer from fire damage – a clear contrast with aboveground structures located within the flame zone that are often heavily damaged by the flames (Choczynska and Johnson, 2009; Hoffmann and Solbrig, 2003; Kavanagh et al., 2010; Pausas et al., 2018). Consequently, how plants experience fires is strongly dependent on their allocation to above- and/or perennial organs positioned belowground.

Many plant species from fire-prone ecosystems have traits that allow them to resprout and persist after fire (Bond and Midgley, 2001), such as the development of new branches mostly from buds located above- and/or belowground (Burrows, 2002; Clarke et al., 2013; Klimešová & Klimeš, 2007). While belowground resprouting is very common (Pausas et al., 2016; Pilon et al., 2021; Zupo et al., 2021), aboveground resprouting usually occur high in the canopy most often in tall trees (Chiminazzo et al., 2021; Scalon et al., 2020; Souchie et al., 2017). Species with this latter strategy usually pay a high cost to protect their trunk (e.g., by producing considerable amounts of bark; Pausas, 2015; Rosell et al., 2014), but gain the ability to maintain a large storage compartment aboveground, allowing to display new foliage in higher strata when compared to species that have resprouted from the ground (Crisp et al., 2011). On the other hand, species with a strategy based on basal and belowground resprouting are assumed to minimize costs of protecting their aerial parts: they rely on both the maintenance of a viable bud bank at the plant base and belowground through the development of perennating organs that can store reserve either at the soil surface or belowground (Pausas et al., 2018).

Aboveground, bark plays a key role in woody plants for protecting their structures from fire. The bark creates a protective layer that surrounds vital inner tissues and insulates them from air, fire, cold, and pathogens (Burrows and Chisnall, 2016; De Antonio et al., 2020; Gashaw et al., 2002; Lawes et al., 2013; Rosell et al., 2021). During a fire event, bark notably prevents the heat from killing the cambium and inducing xylem deformation (Gashaw et al., 2002; Hacke et al., 2001; Lawes et al., 2013, 2011; Michaletz et al., 2012); it also protects buds located below its surface allowing future resprouting (Bond and Midgley, 2001; Burrows, 2002; Charles-Dominique et al., 2015; Chiminazzo et al., 2021). In ecosystems with fires fueled by grasses (e.g., savannas), fires are of low intensity and high frequency (Archibald et al., 2018; Bond and Parr, 2010). Hence, in savannas, the main survival strategy of woody species is to produce and accumulate bark fast enough (without bark shedding) before the next fire event to protect their aboveground parts, instead of accumulating a large amount of bark over a long period (Charles-Dominique et al., 2017). Bark is such an important trait for species from fire-prone ecosystem that it can predict community assembly across fire-sensitive forests and fire-prone savannas based on how much bark woody species produce (at least 0.13 mm of bark per growth unit in the Cerrado; Chiminazzo et al., 2023a; also see Charles-Dominique et al., 2017).

While bark is important for woody species to protect their aboveground organs, developing perennial belowground organs also accounts for the success of plant species during their development in fire-prone ecosystems (Klimešová and Klimeš, 2007; Maurin et al., 2014; Ott et al., 2019). These organs are related to different functions: in addition to bear buds that will assure post-disturbance resprouting, they can allow clonal growth through lateral spread (as in the case of woody rhizomes), assure a large part of resource storage, improve anchorage, and organize the fine roots involved in resource acquisition (Archibald et al., 2018; Bardgett et al., 2014; Klimešová and Klimeš, 2007; Laliberté, 2017; Maurin et al., 2014; Ott et al., 2019). In disturbance-driven ecosystems, the presence of bud-bearing underground storage organs (USOs) is a key trait assuring plant survival and persistence and accounting for vegetation resilience (Bombo et al., 2022; Pilon et al., 2020; Zupo et al., 2021), with belowground resprouting being 25 times more common than aerial resprouting in the Cerrado (Chiminazzo et al., 2021). Moreover, USOs are also important for species capable of resprouting aboveground as they allow resprouting to occur after the aerial structures were consumed or heavily damaged by the flames. Consequently, USOs allow plants' persistence in the post-fire ecosystem even after their aerial buds were damaged by the flames (Charles-Dominique et al., 2015; Grady and Hoffmann, 2012; Souchie et al., 2017). However, even though there are several advantages for plants investing in belowground biomass, there are drawbacks when it comes to resprouting, since basal resprouting requires more time and resources to reconstitute an equivalent biomass and the plant's spatial occupation prior to the disturbance (Clarke et al., 2013; Crisp et al., 2011)

Interestingly, few studies analyzed whether developing USOs trade-off with protecting aboveground structures or not. If having USOs does not preclude protecting the aboveground structures by positioning the buds deep under the bark layer and/or developing a thick bark (Burrows et al., 2010; Charles-Dominique et al., 2015; Chiminazzo et al., 2021), an allocation trade-off is expected as both developing thick bark and large belowground organs incur high costs (e.g., Dantas et al., 2013; Dantas & Pausas, 2013; Gignoux et al., 1997; Lawes et al., 2013; Pausas et al., 2018). Several woody plants have been reported for resprouting both below and aboveground buds after fire (Charles-Dominique et al., 2015; Chiminazzo et al., 2021; Scalon et al., 2020; Souchie et al., 2017), suggesting that under certain conditions, a strategy based on paying costs to both aboveground protection and belowground storage could emerge. Based on these observations, we ask: are species with underground storage organs also protecting their aboveground structures with bark? Does this protection vary according to the type and main function of these organs? For instance, would species with woody rhizomes capable of spreading laterally display different bark production/aerial bud protection when compared to those persisting on spot through organs like the xylopodium and the root crown?

Considering the importance of investing in aboveground and belowground perennial organs for species from fire-prone ecosystems, in this study we tested if

i. species with specialized bud-bearing belowground organs also produce enough bark to allow them to persist in fire-prone ecosystems in the Cerrado (at least 0.13 mm/growth season; Chiminazzo et al., 2023a)
ii. bark production differs according to the type of specialization of the underground storage organ (lateral spreading vs on spot persistence)

We assessed the bark production, aboveground bud protection and potential height of 24 Cerrado woody species that develop common types of underground storage organs with different ecological specialization: woody rhizome (lateral spread), xylopodium and root crown (on spot persistence).

2. Materials and Methods

2.1 Study area

The Cerrado (tropical savanna in Brazil) is composed of different vegetation types ranging from fire-prone savannas and grasslands to fire-sensitive forests (Coutinho, 1978; Eiten, 1972). Fire is closely related to the evolution of plant species of the Cerrado and imposes a strong filter promoting fire-adapted species in savannas (Coutinho, 1990; Dantas, Batalha, et al., 2013; Eiten, 1972; Hoffmann et al., 2012; Simon et al., 2009). For this study, we sampled species at the Santa Bárbara Ecological Station (SBES, 22º48’59’’ S, 19º14’12’’ W), in southeastern Brazil. This protected area is composed of different fire-prone savanna vegetation types (Melo and Durigan, 2011; Ribeiro and Walter, 2008), from *campo sujo* (open savanna) to *cerrado sensu stricto* (woody savanna), as well as fire-free vegetation types like the *cerradão* and the seasonally semideciduous forests. The vegetation at the SBES is exposed to the markedly seasonality of the Cerrado, experiencing hot and wet summers from October to April (mean annual temperature: 24 ºC, total rainfall: 1,000 mm) and dry and mild winters from May to September (mean annual temperature: 18.6 ºC, total rainfall: 400 mm; Melo & Durigan, 2011).

2.2 Species selection and traits description

We compiled information from different sources to select Cerrado woody species i) occurring in fire-prone and open-canopy ecosystems; ii) with underground storage organ type described (Pausas et al., 2018; Pilon et al., 2020; and personal observations); iii) and with information about their bark growth rate and aerial bud protection from our previous studies (Chiminazzo et al., 2021; Chiminazzo et al., 2023a). In our previous studies, we sampled at least three individuals of each species depending on their presence in sampled plots across different savannas. We standardized the nomenclature for underground storage organ types following Pausas et al. (2018). Following the criteria, we were able to describe 24 woody species (Table 1) with three different types of belowground bud-bearing organs (Pausas et al., 2018): i) *xylopodium*, a woody basal swelling that usually origins from the hypocotyl and carries axillary or adventitious buds near the soil surface; ii) *root crown*, defined by the root-shoot transition zone that carries dormant axillary buds grouped in clusters above the soil surface, and iii) *woody rhizome*, a long woody stem distributed horizontally under the soil surface that carry buds mainly concentrated on the nodes (Figure 1).

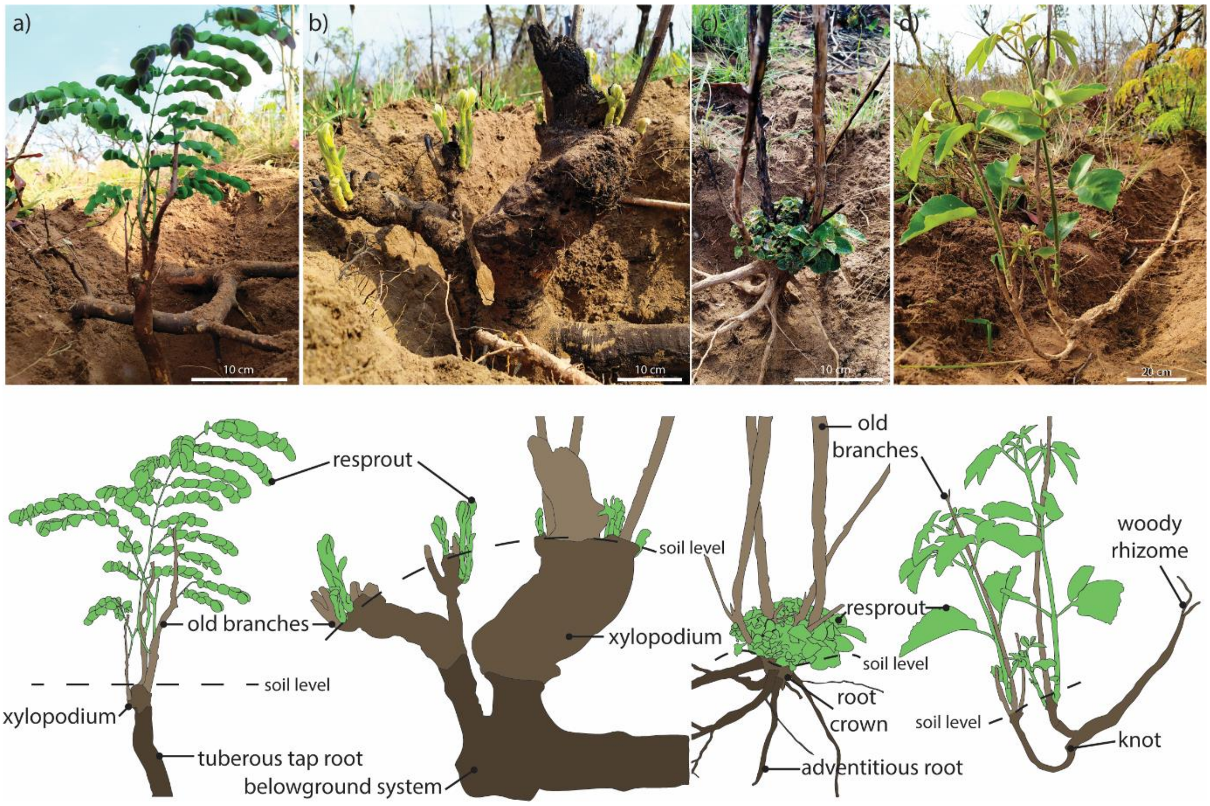

Figure 1 Types of belowground bud-bearing organs. a) Xylopodium associated with a tuberous tap root in *Stryphnodendron rotundifolium.* b) *Annona crassiflora* exhibiting a xylopodium and an unidentified belowground system (note that although not visible in the figures, the belowground system is extensive in the lower soil horizons, perpendicularly to the xylopodium). c) *Miconia albicans* with a root crown and associated adventitious roots. d) *Handroanthus ochraceus* exhibiting a woody rhizome. Scale bars are shown in white at the right bottom of each photo. Dashed lines indicate soil surface.

We then assessed the degree of aerial bud protection for each species as described in Chiminazzo et al. (2021) and De Antonio et al. (2020). This index informs how well the aerial buds are protected by bark based on a scale ranging from zero (unprotected buds) to three (buds fully covered by bark), with intermediate values (1 and 2) based on how deep the buds or the apical meristem are located within the bark layer (Burrows, 2002; Charles-Dominique et al., 2015; Wigley et al., 2020). For one additional taxon (*Erythroxylum cuneifolium*), we determined the bark growth rate by sampling three individuals growing in an open savanna and following the same methodology as in Charles-Dominique et al. (2017): measuring the thickness of every tissue external to the cambium and dividing it by the number of visible growth rings or by the number of well-developed growth units at the measured section of branches, selected to have an analogous morphology to the main stem (Wigley et al., 2020). Finally, we retrieved information from literature and herbaria about the maximal height of each species (except for *Pouteria subcaerulea* that was recorded visually in our study site).

2.3 Statistical analyses

We used generalized mixed effect models (GLMM) to model the variation in bark growth rate (BGR) depending on the type of underground storage organ (USO; xylopodium, root crown, or woody rhizome). We considered the BGR as a response variable, the type of USO as a predictor variable, and the species and their individuals as a random effect. We also used GLMM to model how BGR changes across different species displaying the same type of USO, and across every species regardless of the type of USO. In these two cases, we considered the species as a fixed effect and their individuals as a random effect. After testing the significance of the models, we performed pairwise comparisons between each type of USO and each species displaying the same type of USO. Due to multiple testing across contrasts in these cases, we adjusted the p-values by using the Bonferroni correction method to avoid the type 1 error. The same approach was used to test differences in bark production depending on the specialization of each type of organ (lateral spread or on spot persistence).

After checking that BGR indeed varied depending on the type of USO, we performed a principal component analysis (PCA) to visualize if changes in the BGR would be related with each species aerial bud protection (IBP), their maximum height, and their belowground functional syndromes (persisting fire on spot or spreading laterally). The PCA was carried out using the *factoextra* (v 1.0.7) package, while GLMMs were modeled and tested using the *lme4* (v 1.1.29), *lsmeans* (v 2.30.0), and *emmeans* (v. 1.7.3) packages. All analyses were performed in the R environment using the R software (v. 4.2.0; R Core Team, 2023).

3. Results

Bark production varied from 0.06 to 0.90 mm/growth unit among all species (Table 1). Bark growth rate differed among the species ($P < 0.001$) and among species with the same type of belowground organ ($P < 0.001$). Mean bark production differed across the three types of belowground organs ($P < 0.001$, Table 2). Species with xylopodium showed a mean bark production of 0.23 ± 0.17 mm, while species with root crown had mean bark production of 0.36 ± 0.25 mm and species with woody rhizome displayed bark production of 0.57 ± 0.23 mm/growth unit. A significant difference was detected across organs with different ecological specialization, with bark growth rate and aerial bud protection differing between species with woody rhizome (lateral spread) and xylopodium ($P < 0.001$) and root crown ($P < 0.001$, both on spot persistence) but not between the xylopodium and the root crown organs. Lastly, the ordination of species concerning their growth strategy (on spot or spreading laterally) revealed a clear division explained by their bark growth rate, their aerial bud protection, and the species potential height, with the principal components explaining 92,4% of all data variation (Figure 3).

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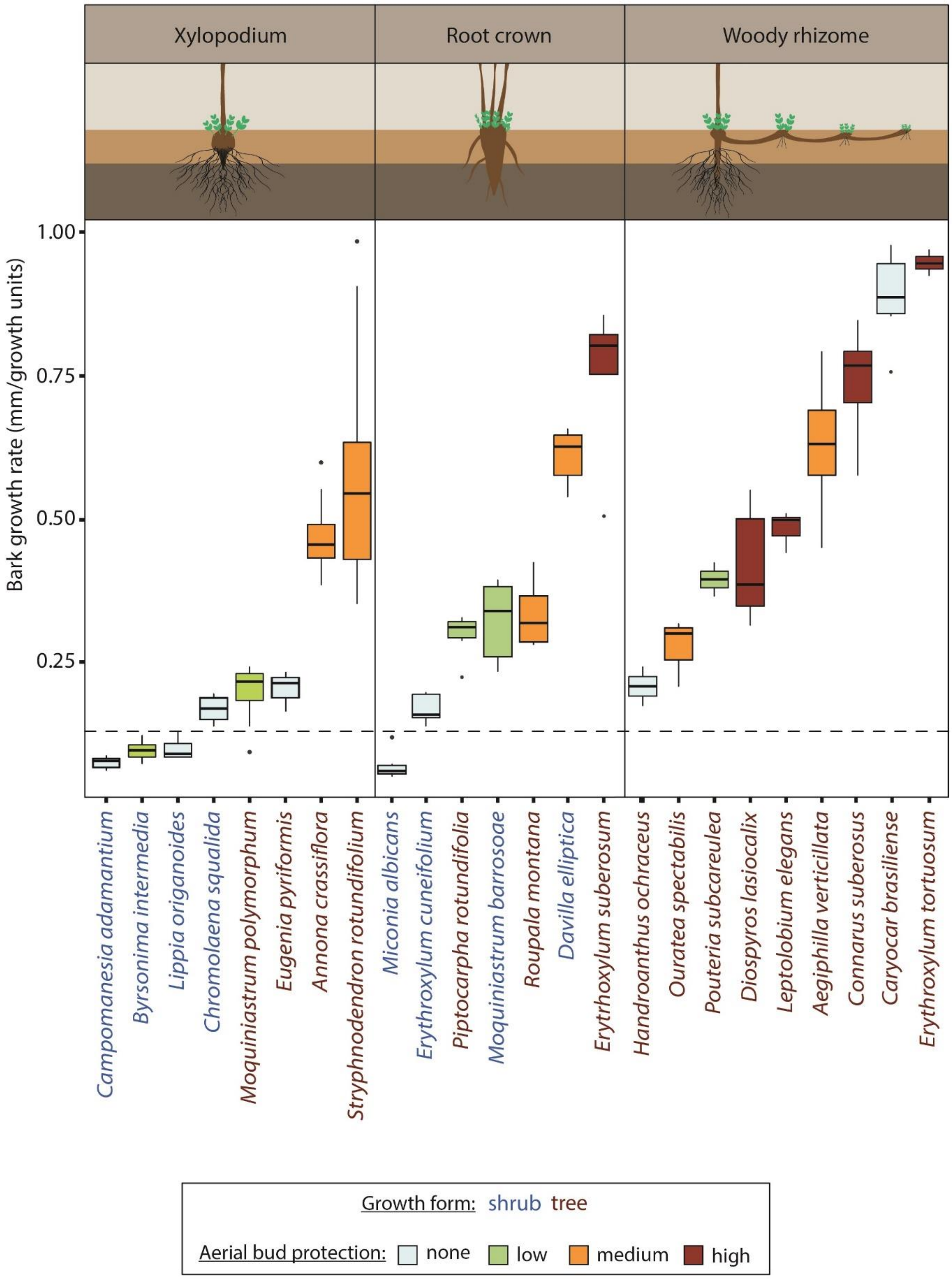
Table 2 Relationship between underground storage organs (predictors) and bark production. Estimates, confidence interval (CI), and their respective p-values (p) are shown, as well as marginal and conditional R^2 values of the model.

	Bark production		
Predictors	*Estimates*	*CI*	*p*
Intercept	0.37	0.20 — 0.53	<0.001
Woody rhizome	0.21	-0.01 — 0.44	0.065
Xylopodium	-0.13	-0.35 — -0.09	0.244
Marginal R²/ Conditional R²	0.269 / 0.896		



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270 **Figure 2:** Bark growth rate according to the species and their belowground organ

271 (xylopodium, woody rhizome, and root crown), their predominant growth form (shrub

or tree) and their aerial bud protection provided by bark (none, low, medium, or high; Chiminazzo et al., 2021; Wigley et al., 2020). The red dashed line indicates the bark threshold separating species from fire-sensitive to fire-prone ecosystems in the Cerrado (0.13 mm; Chiminazzo et al., 2023a). This threshold relates to the minimal amount of bark produced by woody communities capable of persisting in fire-prone ecosystems. Species names are colored according to their predominant growth form (blue = shrubs, brown = trees). USOs illustrations were adapted from Pausas et al. (2018).

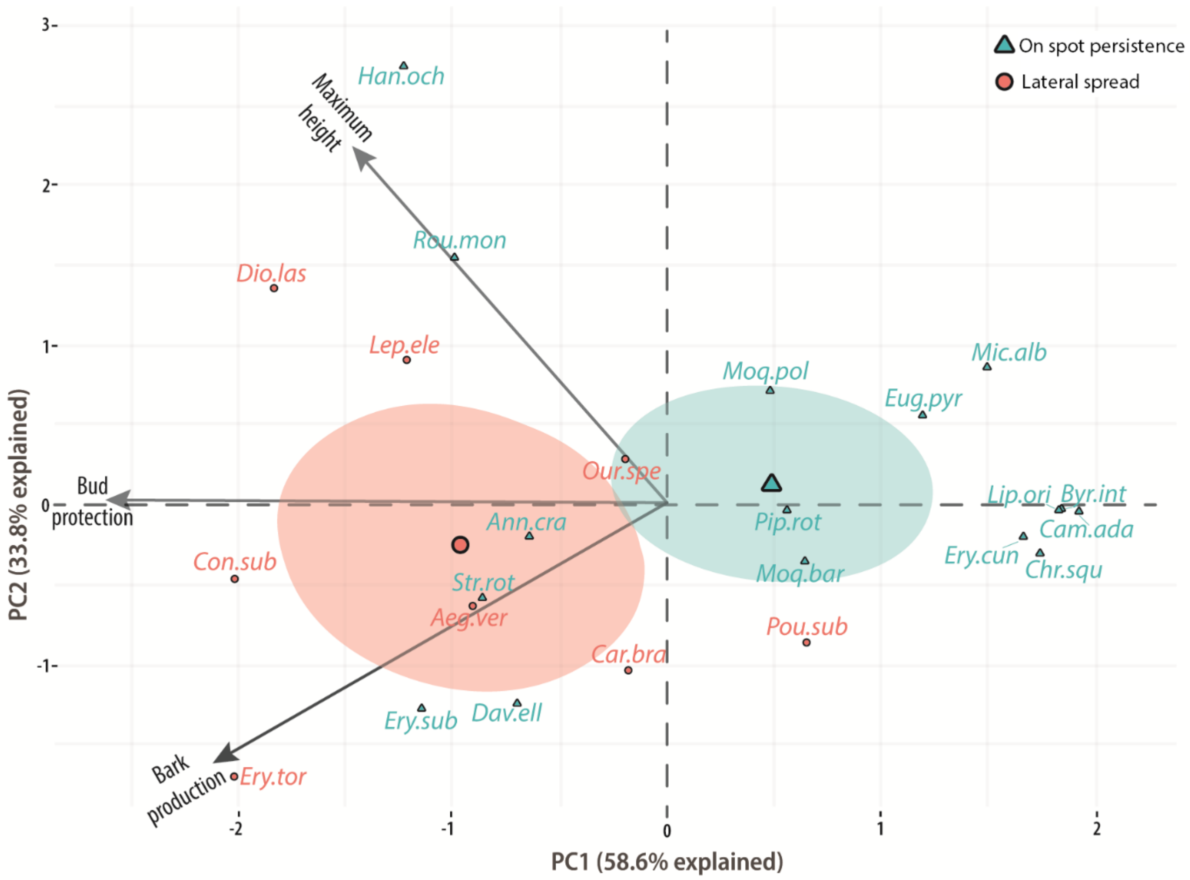

Figure 3: Distribution of species with different types of aboveground strategies (on spot persistence or lateral spread) according to i) their aerial bud protection by bark, ii) their aerial bark production and, iii) their maximum height (i.e., potential height

obtained from herbaria records). The ellipses represent a confidence level of 95% of the centroid calculated using the mean values of the principal components for each category (lateral spread or on spot persistence).

4. Discussion

The results of this study reveal that escaping fire belowground and resisting the flames aboveground are strategies that can occur mutually across different types of underground storage organs (USOs). We demonstrate that the ecological specialization of the belowground organ matters for understanding the strategies being adopted by these plants, as species persisting on spot showed less aboveground protection than those spreading laterally and displaying higher potential height. Consequently, these observations raise further questions: why protect stems from fire when these species are already safe from fire damage? And if there is no major constraint to do so, why do not all plants perform both aerial and belowground protection? In the following we discuss what these differences mean for species from fire-prone ecosystems in the Cerrado and why plants displaying both below and aboveground protection reveal that species are highly adapted to fire.

Bark production differs among species displaying the same type of underground storage organ. An impressive variation of bark growth rate was found among species, varying from 0.06 and 0.90 mm/growing unit, which should translate into different levels of protection of the aboveground tissues against fire (Charles-Dominique et al., 2017; Pellegrini et al., 2017). Interestingly, each USO type comprised species with their bark production distributed all along the gradient from low to high levels of bark protection aboveground. This suggests that species can allocate resources to both develop thick bark aboveground and invest in bud-bearing underground storage organs – at least in the Cerrado, where fire is the main disturbance in open ecosystems (Dantas et al., 2016; Hoffmann et al., 2012). We suggest that by doing so, species can maintain both an above- and belowground viable bud bank, being able to resprout whichever situation is met: if fires are less severe, aboveground resprouting may occur, while if fires are more severe and plants are top-killed, their persistence will be assured by resprouting from the belowground/basal bud bank (Chiminazzo et al., 2021; Clarke et al., 2013), being very difficult to kill a savanna woody species in the Cerrado

Species with a xylopodium (on spot persistence) showed overall a lower bark production when compared to species that developed woody rhizomes (lateral spreading). Root crown species had both low and high bark production and intermediate levels of aerial bud protection (their bud protection was intermediate between species with xylopodium and species with woody rhizomes). Each of the USO type has different level of protection from fire (Pausas et al., 2018): buds are exposed to flames in species with root crowns as they are directly located at the soil surface; by comparison, basal buds of xylopodium are protected from flames located below the soil surface (up to 10 cm deep). For species with root crown, having extra protection aboveground is therefore advantageous, while species with xylopodium have greater chance to resprout after fire since their buds are better insulated from the flames.

Together with bark production, aerial bud protection by bark also differed among species displaying lateral spread and those persisting on spot. In this study, most Cerrado species sampled with woody rhizomes (lateral spread) are single-stemmed trees or treelets, different from species with xylopodium or root crown that often grow as multi-stemmed shrubs. Species with rhizomes had the greatest potential height. The need for thick bark and better bud protection is probably higher in woody rhizome that have a notably smaller bud bank than species with xylopodium and root crown (Bombo et al., 2022); conversely, species with xylopodium and root crown have a greater chance of resprouting from belowground – which in turn help explaining their multi-stemmed architecture (e.g., Götmark et al., 2016; Scheffer et al., 2014; Chiminazzo et al., 2023b). On the other hand, likely compensating for the smaller bud bank, species with woody rhizomes showed to better protect their aboveground buds with bark and position them outside the flame zone. We advocate that this strategy is beneficial for species with woody rhizomes, since they can colonize a greater space in the ecosystem (Klimešová et al., 2018) while maintaining their branches and stems better protected from the flames in taller strata (Chiminazzo et al., 2021; Crisp et al., 2011). These observations combined with their greater potential height suggest that these species are more likely to eventually escape the firetrap (see Bond and van Wilgen, 1996).

Although Cerrado woody plants can produce great amounts of bark, investing in bark aboveground does not necessarily mean branch capacity of surviving fire. This capacity relies on different traits that confer thermal insulation during fire events, like branch and bark density, inner bark proportion in relation to the outer bark, bark water content, and stem diameter (Hacke et al., 2001; Hoffmann et al., 2012; Kavanagh et al., 2010; Lawes et al., 2011; Loram-Lourenço et al., 2020; Pausas, 2015; Rosell et al., 2021, 2014; Scalon et al., 2021). According to Chiminazzo et al. (2023), a minimum of 0.13 mm of bark production is enough to differentiate species from fire-prone and fire-sensitive ecosystems in the Cerrado. However, this does not indicate that all species producing bark above the threshold are able to have their aerial parts well-protected against fire: some species produce bark above the threshold, but their stems rarely reach enough diameter to survive fire (e.g., *Chromolaena squalida*, *Lippia origanoides*) – thus often being top killed and resprouting from belowground. Therefore, further studies should address experimental approaches combining bark production with plant architecture and allometry to better disentangle bark production from growing and resprouting patterns.

Finally, the results of this study highlight the importance of considering belowground traits when studying plant functional differentiation (e.g., Bardgett et al., 2014; Klimešová et al., 2018; Laliberté, 2017; Ott et al., 2019). Taking into account the morphology of belowground organs (i.e., where and how the buds are protected) together with aboveground traits (here, bark production and aerial bud protection), showed to relate with the type of growing strategy that plants display in the Cerrado fire-prone ecosystems (persisting on spot or spreading laterally) and to how much of biomass they invest aboveground through their potential height. Although trade-offs are often expected concerning alternative strategies, e.g., either escaping or resisting the flames (Dantas & Pausas, 2013), our results suggest that species combining several fire-survival strategies might also be selected in fire-prone ecosystems.

5. Conclusions

The great variation in rates of bark production aboveground throughout different types of bud-bearing underground storage organs indicate that Cerrado woody species invest in strategies that confer both above- and belowground protection against fire, allowing them to persist both if fires are more or less severe. Therefore, escaping the ‘firetrap’ can be combined with resisting the flame action, as Cerrado species are both fire-resisting aboveground (through investments in bark and aerial bud protection) and fire-escaping belowground (by hiding buds in organs belowground). Further studies should quantify which strategies are being promoted under different fire regimes and how they may impact vegetation feedbacks.

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7. Author contributions

AF conceived and designed the study. MAC wrote the original draft and led the writing of the manuscript. MAC, ABB, and AF performed field sampling. MAC and TC-D analyzed the data. All authors participated actively in the execution of the study and gave final approval for publication.

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9. Figure captions

Figure 1 Types of belowground bud-bearing organs. a) Xylopodium associated with a tuberous tap root in *Stryphnodendron rotundifolium.* b) *Annona crassiflora* exhibiting a xylopodium and an unidentified belowground system (note that although not visible in the figures, the belowground system is extensive in the lower soil horizons, perpendicularly to the xylopodium). c) *Miconia albicans* with a root crown and associated adventitious roots. d) *Handroanthus ochraceus* exhibiting a woody rhizome. Scale bars are shown in white at the right bottom of each photo. Dashed lines indicate soil surface.

Figure 2: Bark growth rate according to the species and their belowground organ (xylopodium, woody rhizome and root crown), their predominant growth form (shrub or tree) and their aerial bud protection provided by bark (none, low, medium, or high; Chiminazzo et al., 2021; Wigley et al., 2020). The red dashed line indicates the bark threshold separating species from fire-sensitive to fire-prone ecosystems in the Cerrado (0.13 mm; Chiminazzo et al., 2023a). This threshold relates to the minimal amount of bark produced by woody communities capable of persisting in fire-prone ecosystems. Species names are colored according to their predominant growth form (blue = shrubs, brown = trees). USOs illustrations were adapted from Pausas et al. (2018).

Figure 3: Distribution of species with different types of aboveground strategies (on spot persistence or lateral spread) according to i) their aerial bud protection by bark, ii) their aerial bark production and, iii) their maximum height. The ellipses represent a

confidence level of 95% of the centroid calculated using the mean values of the principal components for each category (lateral spread or on spot persistence).