Bark production of generalist and specialist species across savannas and forests in the Cerrado

Marco Antonio Chiminazzo, Aline Bertolosi Bombo, Tristan Charles-Dominique, Alessandra Fidelis

To cite this version:

Marco Antonio Chiminazzo, Aline Bertolosi Bombo, Tristan Charles-Dominique, Alessandra Fidelis. Bark production of generalist and specialist species across savannas and forests in the Cerrado. Annals of Botany, 2023, 131 (4), pp.613-621. 10.1093/aob/mcad014 . hal-04047093

HAL Id: hal-04047093

https://hal.inrae.fr/hal-04047093v1

Submitted on 24 Oct 2023

Original Article

Bark production of generalist and specialist species across savannas and forests in the Cerrado

Running title: Bark growth rate across savanna-forest mosaics in the Cerrado

Marco Chiminazzo[1]*, Aline Bertolosi Bombo[1], Tristan Charles-Dominique[2,3], Alessandra Fidelis[1]

[1] Lab of Vegetation Ecology, Universidade Estadual Paulista (UNESP), Instituto de Biociências, Avenida 24-A, 1515, Rio Claro, 13506-900, Brazil.

[2] AMAP, Univ Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France.

[3] Institute of Ecology and Environmental Sciences – Paris CNRS UMR 7618, Sorbonne University, Paris, France.

Author for correspondence: Marco Chiminazzo

marco.chiminazzo@unesp.br, marcochiminazzo@gmail.com, Universidade Estadual Paulista (UNESP), Instituto de Biociências, Avenida 24-A, 1515, Rio Claro, 13506-900, Brazil)

Summary

- **Background and Aims** Bark allows species to survive fire, protecting their inner tissues and allowing new branches to resprout from aerial buds. Thus, bark production is likely to be selected with aerial bud protection in fire-prone ecosystems. By considering the coexistence of fire-prone and fire-free ecosystems, and the different impacts of flames over different growth forms, in this study we tested whether a) species from areas with higher fire frequencies have a faster bark production, b) bark growth rate differs between trees and shrubs; c) generalists adjust their bark production according to their environment (fire-prone or fire-free), and d) a fast bark production results in a better aerial bud protection.
- **Methods** We sampled two different types of forests and savannas in the Cerrado and registered every woody individual with height between 1.5 and 3 m tall (directly exposed to the flames). Then, for the 123 species registered, we sampled three different individuals in each vegetation type that the species occurred to assess their bark production and aerial bud protection. We then checked each species habitat of preference (savanna and forest specialists or generalists) and their predominant growth form.
- **Key Results** A minimal threshold of 0.13 mm/growth unit of bark production differentiated woody communities from savannas and forests. Shrubs and trees did not differ in terms of bark growth rate, although being exposed differently to the flames. Generalist species in savannas were able to produce bark above the threshold. However, when these species were in forests, they produced bark below the threshold. Finally, a higher bark growth rate accounted for a better aerial bud protection.
- **Conclusions** Generalist species are likely capable of displaying plasticity on their bark production, which can be important for their success in contrasting ecosystems.

The relationship between aerial bud protection and bark growth rate suggests that bark production plays an important role in protecting the dormant buds, as well as being selected in fire-prone ecosystems.

Keywords: bark growth rate, bark thickness, bud protection, fire, savanna-forest boundaries, neotropical savannas, persistence niche, resprouting.

INTRODUCTION

Savannas have a continuous flammable grass layer that supports frequent fires, creating a harsh environment for trees to persist as their aboveground parts are exposed to flames (Bond, 2013). In contrast, forests present a continuous tree canopy, which shades out flammable grasses (Hoffmann et al., 2012; Charles-Dominique et al., 2018). Tropical savannas and forests are distributed in mosaics mostly maintained by fire (Staver et al., 2011; Pausas, 2015a), which selects species capable of persisting in fire-prone ecosystems (Rossatto et al., 2009; Hoffmann et al., 2012; Charles-Dominique et al., 2015a; Lamont et al., 2019). Bark thickness of woody species is a key trait that enables their survival during fires by protecting the inner tissues of the stem from the flames and the heat (Lawes et al., 2013; Rosell et al., 2014; Pausas, 2015b), thus allowing the species to resprout new branches from their aerial buds (Bond and Midgley, 2001; Clarke et al., 2013).

Bark tissues are responsible for providing mechanical and chemical protection to the plant inner living tissues and to meristematic regions responsible for the plant regeneration (Burrows, 2002; VanderWeide and Hartnett, 2011; Hoffmann et al., 2012; Schafer et al., 2015; Scalon et al., 2020). Bark is not only important for insulating vital tissues, but also for storing important resources like nonstructural carbohydrates which are fundamental for resprouting post-fire (Clarke et al., 2013; Rosell et al., 2021). In fire-prone ecosystems, the rate at which bark is produced (*bark growth rate* hereafter) is crucial for species persistence, as it determines their capacity to accumulate enough bark between fire events (VanderWeide and Hartnett, 2011; Schafer et al., 2015; Charles-Dominique et al., 2017; Wigley et al., 2020).

In flammable ecosystems, woody plants are expected either to prioritize a fast vertical growth when fires are less frequent and less intense (Lanky strategy) or to prioritize a fast bark growth rate when fire is more frequent and intense (Corky strategy; Dantas and Pausas, 2013). Neotropical savannas are largely dominated by plants with the Corky strategy, thus accounting for a greater bark investment when compared to Afrotropical savanna woody species (Dantas and Pausas, 2013). However, different growth forms - like trees and shrubs - coexist in those areas. This coexistence is puzzling: while trees can grow their canopy above the flame height and escape the firetrap, shrubs complete all their developmental stages within the flame zone due to their lower stature. These differences suggest that low and high statured plants (i.e., shrubs and trees) would require very different rates of bark production with strong implications over their allocation strategies.

In frequently disturbed environments, the fitness of plants can depend much more on surviving in early stages than outcompeting neighbors or reproducing abundantly (Bond and Midgley, 2001); with species often relying in bud protection and bark production to persist in the environment (Clarke et al., 2013; Pausas, 2015b; Pausas et al., 2018). Previous investigations in African savannas revealed that bark growth rate and bud protection are not strongly correlated, suggesting that buds are not simply passively buried under bark but instead maintained actively in or out the bark layer over time (Charles-Dominique et al., 2017). Further, the two traits could be expressed in combination to promote fire resistance and to enhance resprouting capacity. As these first observations were made in African vegetation that faces less intense fires than the Cerrado (a species-rich, tropical savanna located in Brazil, where fire is one of the major drivers maintaining the mosaics of savannas and forests; Dantas and Pausas, 2013; Charles-Dominique et al., 2017), here we investigate whether these two traits (aerial bud protection and bark growth rate) are more frequently combined in neotropical species exposed to more intense grass fires than those from the Afrotropical savannas.

Although woody communities from savannas and forests differ in composition and structure, some species can inhabit both environments (generalists). We distinguish them from specialist species that cannot overcome the environmental barrier between forest and savanna and are restricted to a single habitat type (Futuyma and Moreno, 1988). When strong environmental filters such as fire and shade select species and assemble communities, very contrasted strategies are selected and filtered at the both ends of the spectrum (Hoffmann et al., 2012; Charles-Dominique et al., 2015b; 2017). In the presence of such filters, observing generalist species is particularly interesting as their presence in both ecosystems either means that their biology includes a unique combination of traits that allow them to survive in both ecosystems or they adopt a plastic behavior allowing them to overcome the environmental barrier. Do they optimize bark production to have enough to survive fire but not too much with costs compatible with shaded environments (e.g., “jack-of-all-trades-master-of-none”; MacArthur, 1961)? Or can they adjust their bark production according to the habitat they are developing in, thus behaving like specialists of both systems (e.g., “jack-of-all-trades-master-of-some”; Richards et al., 2006)?

Both bark production and aerial bud protection are important traits for species survival in fire-prone ecosystems, but to which extent they interact influencing communities and species across contrasting habitats and growth forms needs further investigation. In this study we address these points by exploring four different questions: (i) We first investigate whether species are selected by fire frequency according to their bark growth rate in neotropical savanna-forest mosaics; (ii) second, we explore whether generalist species adjust their bark production according to their growing environment; (iii) third, we test whether bark production differ between species with different predominant growth forms (specifically trees and shrubs that have their aerial biomass exposed differently to the flames). (iv) Last, we test whether a greater bark production is linked to a better aerial bud protection.

MATERIALS AND METHODS

Study area

We conducted the study at the Santa Bárbara Ecological Station (SBES, 22º48’59’’ S, 49º14’12’’ W, 589 m.a.s.l.), a protected area in southeastern Brazil that comprises a wide diversity of co-existing vegetation types. Mean temperature ranges from 18 to 22 ºC and mean annual rainfall from 1,000 to 1,300 (Melo and Durigan, 2009). Climate is seasonal, with a wet and hot summer and a dry and mild winter. We selected four different vegetation types with contrasted fire frequencies (fire events calculated over from 1984 to 2018; Conciani et al, 2021): i) *open savannas*, high fire frequency with 5-9 fire events; defined by high grass cover (up to 80%) co-occurring with short tress and scattered shrubs; ii) *woody savannas*, low fire frequency with 0-2 fire events; characterized by a lower grass cover (up to 50%) and taller trees capable of suppressing the continuous grass layer by shading locally; iii) *cerradão*, no fire event; forests composed of a mix of generalists (species occurring in both savannas and forests) and dry forest species; and iv) *seasonal semi-deciduous forest*, no fire event; forests composed of tall tree species of the Atlantic Rainforest (Fig. **1**, Coutinho, 1990).

Sampling design and study species

We randomly established 10 transects of 10 x 40 m in each vegetation type. We registered every woody individual with a height between 1.5 and 3 m, because within this height different growth forms (trees and shrubs) are exposed to the flames, thus creating a bottleneck that woody species must overcome to persist in the environment. For each sampled species within the transects, we collected three to five branches from three different individuals in every vegetation type they occurred and scored the predominant growth form according to Abreu et al. (2017) and Flora do Brasil (2020).We then classified every species as savanna exclusive, forest exclusive, or generalists (species that inhabits at least one savanna and one forest vegetation) according to Abreu et al. (2017) and Flora do Brasil (2020). To compare the bark production of generalist species growing into forests and savannas, we analyzed ten different species that were sampled in at least one savanna and one forest in our study area: *Copaifera langsdorffii* Desf. (Fabaceae), *Erythroxylum pelleterianum* A.St.-Hil. (Erythroxylaceae), *Luehea grandiflora* Mart. & Zucc. (Malvaceae), *Moquiniastrum polymorphum* (Less.) G. Sancho (Asteraceae), *Myrcia multiflora* (Lam.) DC. (Myrtaceae), *Pera glabrata* (Schott) Baill. (Peraceae), *Tabernaemontana hystrix* Steud. (Apocynaceae), *Terminalia glabrescens* Mart. (Combretaceae), *Trichilia pallida* Sw. (Meliaceae) and *Vochysia tucanorum* Mart. (Vochysiaceae).

Trait description

We scored the level of bud protection using the Index of bud protection (I_{BP}) after performing at least three observations from three different individuals for each species (Burrows, 2002; Charles-Dominique et al., 2015a). This index informs, from macro-anatomical observations on main longitudinal sections of main branches (morphologically analogous to trunk), about the degree of bud protection, which ranges from 0 (bud fully exposed to fire) to 3 (bud fully covered by bark) (Charles-Dominique et al., 2015a, Fig. **2a**). The index of bud protection for the species in the study area was described in Chiminazzo et al. (2021). We assessed the bark growth rate (BGR) in well-developed branches with similar architecture to the main stem (this method of sampling allows a direct comparison of bark production between single and multi-stemmed species, *i.e.*, trees and shrubs) through transversal sections and considered as bark every tissue external to the wood - cambium region (Wigley et al., 2020). We then counted the number of visible growth rings and photographed the samples under a binocular stereomicroscope. When growth rings were not visible, we considered the number of stem growth units (Barthélémy & Caraglio, 2007; Wigley et al., 2020). Sampled branches had 3.20

± 0.69 growth units and 7.09 ± 2.25 mm of diameter. Bark thickness was then measured at the base of the stems in three different parts through radial sections by using the ImageJ software (Schneider et al., 2012). We then divided the mean bark thickness by the number of growth rings/units of the branch at the given section to obtain the bark growth rate (Charles-Dominique et al., 2017; Wigley et al., 2020). To avoid confounding the rate of bark production with bark shedding, we made sure that no bark was shed at the location of the recorded anatomical section by assessing the presence of dead epidermis out of the outermost bark layer (Charles-Dominique et al., 2017) and collected branches with at least three growth units (Fig. **2a,b**). We tested whether the variation in bark growth rates was explained either by an overall growth of the plant that could be produced in vegetation types with resource limitation (here light) or by a differential allocation to bark that could be related to the fire frequency experienced by species. We did so by comparing the growth rate to the wood growth rate (length of pith plus wood on a transversal section divided by the numbers of growth units), used here as a proxy for the overall growth of the plant. Lastly, to make sure that differences considering the bark growth rate of generalist species were not driven by changes in abundance and composition across vegetation types, we compared the bark production of 10 generalist species sampled in at least one forest and one savanna vegetation.

Statistical analyses

We used generalized linear mixed effect models (GLMM) to analyze how bark growth rate was distributed across vegetation types with different fire frequencies and between species' growth forms (shrubs and trees). We considered sampled individuals as a random effect and the vegetation type and growth form as fixed effects. After testing the significance of fixed effects, we performed pairwise comparisons using post hoc tests of Tuckey type with Bonferroni correction. We used generalized linear models (GLM) to analyze the relationship between bud protection and bark growth rate and between bark growth rate and fire frequency. We then calculated the community-weighted mean values (i.e., the weight of a trait in a given community - CWM) of the bark growth rate in each plot to analyze how the CWM values were distributed along fire frequencies. We then assessed at which threshold woody communities switch from savannas to forests by considering the 1st and the 3rd quartiles of bark growth rate in each vegetation type. GLMs and post-hoc tests as described above were used to test the differences of CWM according to the fire frequency and to compare the variation of wood and bark growth rates across vegetation types and generalist versus specialist species. To test differences in bark production of generalist species sampled in both savannas and forests, we used linear mixed-effects models considering the vegetation type as a fixed factor and the species and their individuals as random effects. To do so, we first obtained each generalist species mean bark production and compared it with the bark production of each individual sampled in savannas and forests. This approach allowed us to obtain the residuals of each individual bark production (translating into bark adjustment across different vegetation types). Lastly, to test differences between shrubs and trees (regardless the vegetation they occur) we performed a Wilcoxon signed-rank test as bark production of both trees and shrubs were not normally distributed (Shapiro-Wilk normality test, $P \leq 0.001$). All analyses were performed on the R software (R Core Team, 2022).

RESULTS

Bark growth rate (BGR) differed between woody communities of forests and savannas. Bark growth rate was greater in species occurring in savannas, with *c*. three-fold faster bark production than forest species ($P \leq 0.001$, Fig. **3a**, Table **1**). Generalist species produced more bark when growing in savanna compared to individuals growing in forest, on average with an additional 0.1 mm of bark per growth unit in savanna compared to forest (P

< 0.01, Fig. **3c)**. No interaction was detected between bark growth rate of different growth forms and among the similar vegetation types (open/woody savanna and cerradão/semi-deciduous forests). Contrary to our predictions, the bark production of trees and shrubs did not differ. However, within each vegetation type, trees showed a tendency of producing more bark than shrubs (Fig. **3b**). Species BGR scores are shown in Supplementary Information (Table S1).

Community-weighted means (CWM) for bark growth rate varied according to fire frequency (Table **1**). Savannas with high fire frequency (*open savannas*, 5-9 fire events) had CWM values of bark growth rate of 0.379 mm/year, while savannas with lower fire frequency (*woody savannas*, 1-2 fire events) showed a CWM of 0.293 mm/year. Forest systems (no fire) showed a CWM of 0.107 mm/year. A shift from forest to savanna communities was found at the first quartile ranking species' bark production in open savannas and the third quartile in the semi-deciduous forest, indicating that a minimum bark growth rate of *c.* 0.13 mm/year is required for species to occur in fire-prone systems (Fig. **3**), thus differentiating communities of forests and savannas ($P \leq 0.001$, Table **1**). Above this threshold, most species occurring in open (33 species, 80% of the community) and woody (40 species, 71%) savannas produce at least 0.13 mm of bark. In forests, only 20 (41%) species from the cerradão and 6 (18%) species from the semi-deciduous forest produced more than 0.13 mm of bark. Out of the 26 species sampled in forest that produced bark above this threshold, 30% are forest specialists, 38% are generalists, and 26% are savanna specialists (in forests, these savanna-specialist species were represented by one or two individuals and were sampled in the cerradão). In savannas, out of the 25 sampled species that produced bark below the threshold, 32% are generalists and 59% are savanna specialists (we did not account species without available information about their habitat of preference and one forest specialist species sampled in the open savanna; Fig. **3a**). The ratio between wood growth rate and bark growth rate differed greatly across vegetation types ($P \leq 0.001$) and between generalists and specialists ($P \leq 0.01$; Fig. S1, Table S2), thus indicating that allocation to bark differed. Lastly, woody individuals with higher degrees of bud protection ($I_{BP} = 2, 3$) produced bark *c*. 2 times faster than individuals with low or no bud protection ($I_{BP} = 0, 1$; Table **1**, $P \leq 0.001$).

DISCUSSION

The results of our study highlight the importance of bark production in selecting species across contrasting environments such as forests and savannas. As expected, we found that bark growth differs across savanna and forest communities, revealing a minimal threshold of bark (0.13 mm/growth unit) that is required to avoid top-kill and that could be facilitating a greater species survival in fire-prone ecosystems. Interestingly, we observed that a greater bark production is combined with a better aerial bud protection – two key traits that improve species persistence in fire-prone ecosystems (Burrows, 2002; VanderWeide and Hartnett, 2011; Hoffmann et al., 2012; Schafer et al., 2015; Charles-Dominique et al., 2017, Chiminazzo et al., 2021). Contrary to our predictions, we did not find any differences considering bark growth rate between shrubs and trees. This is particularly interesting because even though different growth forms experience fire differently (the aboveground structures of shrubs are entirely within the flames, while tree canopies can escape the flame zone), both trees and shrubs are generally required to produce significant amounts of bark when growing into fire-prone ecosystems. Further, we did not find differences in the bark production of generalist and specialist species. This later result further revealed that generalist species possibly rely on a plastic production of bark according to the environment they grow in. In the following, we expand on the implications these results have for the persistence of species in fire-prone ecosystems.

On the importance of bark production for generalist and specialist species in savanna-forest mosaics

Woody species from savannas produce three times more bark than forest woody species, suggesting that a minimum of 0.13 mm of bark production is required to avoid top-kill in fire-prone ecosystems. In fire-free forests, most individuals develop less bark than this threshold. Bark is an important fire-related trait, as it creates a physical barrier against the flames, insulating vital inner tissues from the heat (Rosell et al., 2014; Pausas, 2015b). Accordingly, the rate at which bark is produced is also important in flammable ecosystems, since it determines the capacity of woody plants to have their resprouting stems and young saplings protected before experiencing their first fire event (Charles-Dominique et al., 2017; Wigley et al., 2020). Therefore, the existence of a threshold of bark growth rate between forest and savanna further confirms the role of fire in maintaining savannas and forest as mosaics (Hoffmann et al., 2012; Dantas et al., 2013; Charles-Dominique et al., 2015b) and the importance of bark investment for Cerrado woody species (Hoffmann et al., 2012; Dantas and Pausas, 2013; Scalon et al., 2020; 2021, Loram-Lourenço et al., 2020). We further observed that allocation to bark varied across vegetation types, as the bark growth rates were not following the same variation as wood growth rates (similar variation of rates would indicate that the overall growth of the plant varies according to the growing environment, not its allocation to bark).

When fire is suppressed from savannas, generalist species are usually those contributing the most to the density of woody communities (Flake et al., 2021). These species can produce bark above the threshold at an equal rate as many savanna-specialist species and could develop in savannas where fire is present. Interestingly, generalist species sampled in forests where fire is absent have bark production that is equivalent to forest specialists. This capacity of generalist species to adjust their bark production according to their environment defines them as "jack-of-all-trades-mater-of-some", a strategy that characterizes the most ecologically successful species, such as invasive ones (see Richards et al., 2006). Further studies should focus on the physiological mechanisms explaining this ability to adjust bark production and the associated benefits in terms of cost reduction and increased survival as generalists could have a profound effect on forest-savanna mosaics by allowing transitions between them and induce successional patterns that are not simply driven by increasing shade. Importantly, further investigation could help understand how this bark adjustment is performed by the plant and how it relates to the overall allocation strategies.

Different growth forms, similar bark production? Bark growth rate across trees and shrubs

The bark production of trees and shrubs did not differ in our study area. This result is particularly interesting because we expected the opposite: fire severity is greater at up to 50 cm above the soil surface and reduced below and above this area and drop quickly above the flame height (Clarke et al., 2013; Graves et al., 2014; Rodrigues et al., 2021), species with different growth forms face fire differently by being within or outside the flame zone (Chiminazzo et al., 2021) and should thus display different rates of bark production. Bark production for example varies within the same individual, with bark investment being greater near to the soil when compared to the canopy (Graves et al., 2014; Scalon et al., 2020; Lawes et al., 2021). Therefore, the lack of differences in bark production of trees and shrubs may be an indication that both growth forms must invest in producing bark when growing in fire-prone ecosystems, thus questioning how much of bark production is traded for a short stature (e.g., Dantas et al., 2013; Scalon et al., 2020), at least in areas with frequent fires.

Out of the few species inhabiting savannas and producing bark below the threshold, most of them are shrubs (66%) and savanna specialists (54%), thus suggesting the presence of alternative strategies for shrub persistence in savannas. Strategies other than investing in bark production aboveground, like trichomes covering buds (Chiminazzo et al., 2021) and resprouting from belowground bud-bearing organs were reported for most of these species (Pilon et al., 2021; Zupo et al., 2021; Chiminazzo et al., 2021). Therefore, although bark production is strongly linked to savanna communities, shrub species can trade this strategy by allocating most of their biomass belowground – also allowing them to persist in the post-fire environment (Klimešová and Klimeš, 2007, Pausas et al., 2018; Ott et al., 2019; Pilon et al., 2021; Zupo et al., 2021; Chiminazzo et al., 2021). Hence, bark production alone cannot fully explain the assembly of communities with different growth forms in fire-prone ecosystems.

A greater bark production accounts for a better aerial bud protection

Our results indicate that bark growth rate was strongly related to bud protection. Previous examples on Afrotropical savannas showed that bud protection was only weakly correlated to bark production (Charles-Dominique et al., 2017). A possible reason for these divergences may be differences in fire frequencies and intensities, since the Cerrado is exposed to more intense fires than the Afrotopical savannas (Dantas and Pausas, 2013). However, differences in fire intensities/frequencies may not fully explain the bark production-bud protection relationship: conifers exposed to surface fires (e.g., in the Andes and the western North America) can produce thick bark capable of surviving fires (Pausas, 2015b), but this group of plants can present empty axils and meristems embedded near the bark surface translating into a lower bud protection (Burrows et al., 2003). Conversely, eucalypts are remarkable for expressing the highest bud protection (embedded within the wood) while having very low bark thickness (Burrows, 2002). The relationship between bark production and aerial bud protection should therefore be investigated more widely across different systems and species clades to better understand the ecological meanings of either investing in bud protection, or in greater bark growth rate, or in both.

Conclusions

Bark growth rate is an important trait for sorting woody plant species in savanna and forest mosaics in the Cerrado. In flammable ecosystems, a high bark growth rate is combined with very high aerial bud protection, evidencing that fire is a particularly strong environmental filter selecting species in the Cerrado. The differences in bark production of generalist species question further how plants could adjust their resource allocation to bark depending on the presence of fire or light availability. More studies on the intraspecific variability of fire adaptations are urgently required to understand better how the generalists can bridge two worlds (fire versus shade dominated) and affect the distribution and dynamics of forest-savanna mosaics.

ACKNOWLEDGMENTS

The authors are thankful to Dhemerson Conciani, Gabriela Damasceno, Giovana Chiari, Mariana Dairel, Vagner Zanzarini, Renon Andrade and the staff of Santa Bárbara Ecological Station for their help during the field work. The authors also thank Dr. Davi Rossatto and Dr. Marcelo Simon for suggestions on an early version of this paper. We also thank the three anonymous reviewers and the editors who helped improve this manuscript.

FUNDING

This study was supported by FAPESP (2015/06743-0) and CNPq (406505/2018-7). MAC received financial support from CNPq (134582/2018-7) and FAPESP (2018/21300-6, 2021/09269-9), ABB from FAPESP (2017/02934-1) and AF received grant from CNPq (312689/2021). This study was authorized by the COTEC N. 57/2019 D144/2018 PH.

REFERENCES

Abreu RCR, Hoffmann WA, Vasconcelos HL, Pilon NA, Rossatto DR, Durigan G. 2017. The biodiversity cost of carbon sequestration in tropical savanna. *Science Advances* 3:e1701284.

Barthélémy D, Caraglio Y. 2007. Plant Architecture: A Dynamic, Multilevel and Comprehensive Approach to Plant Form, Structure and Ontogeny. *Annals of Botany* 99:375–407.

Bond WJ. 2013. *Fire and plants*. London: Chapman & Hall.

Bond WJ, Midgley JJ. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution* 16:45–51.

Burrows GE. 2002. Epicormic strand structure in Angophora, Eucalyptus and Lophostemon (Myrtaceae) - implications for fire resistance and recovery. *New Phytologist* 153:111–131.

Burrows GE, Offord CA, Meagher PF, Ashton K. 2003. Axillary Meristems and the Development of Epicormic Buds in Wollemi Pine (*Wollemia nobilis*). *Annals of Botany* 92:835–844.

Charles-Dominique T, Beckett H, Midgley GF, Bond WJ. 2015a. Bud protection: a key trait for species sorting in a forest-savanna mosaic. *New Phytologist* 207:1052–1060.

Charles-Dominique T, Midgley GF, Bond WJ. 2017. Fire frequency filters species by bark traits in a savanna-forest mosaic. *Journal of Vegetation Science* 28:728–735.

Charles-Dominique T, Midgley GF, Tomlinson KW, Bond WJ. 2018. Steal the light: shade vs fire adapted vegetation in forest-savanna mosaics. *New Phytologist* 218:1419–1429.

Charles-Dominique T, Staver AC, Midgley GF, Bond WJ. 2015b. Functional differentiation of biomes in an African savanna/forest mosaic. *South African Journal of Botany* 101:82–90.

Chiminazzo MA, Bombo AB, Charles-Dominique T, Fidelis A. 2021. Your best buds are worth protecting: Variation in bud protection in a fire-prone cerrado system. *Functional Ecology* 35:2424–2434.

Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJE. 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* 197:19–35.

Conciani DE, Santos LP dos, Silva TSF, Durigan G, Alvarado ST. 2021. Human-climate interactions shape fire regimes in the Cerrado of São Paulo state, Brazil. *Journal for Nature Conservation* 61:126006.

Coutinho LM. 1990. Fire in the Ecology of the Brazilian Cerrado. *Fire in the Tropical Biota*. Ecological Studies, Goldammer JG (ed) Springer Berlin Heidelberg, Berlin, Heidelberg, p 82–105

Dantas V de L, Batalha MA, Pausas JG. 2013. Fire drives functional thresholds on the savanna–forest transition. *Ecology* 94:2454–2463.

Dantas V de L, Pausas JG. 2013. The lanky and the corky: fire-escape strategies in savanna woody species. *Journal of Ecology* 101:1265–1272.

Flake SW, Abreu RCR, Durigan G, Hoffmann WA. 2021. Savannas are not old fields: Functional trajectories of forest expansion in a fire-suppressed Brazilian savanna are driven by habitat generalists. *Functional Ecology* 35:1797–1809.

Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro. Available at <http://floradobrasil.jbrj.gov.br>. Accessed on 06 Jan. 2023.

Futuyma DJ, Moreno G. 1988. The Evolution of Ecological Specialization. *Annual Review of Ecology, Evolution and Systematics* 19:207–233.

Graves SJ, Rifai SW, Putz FE. 2014. Outer bark thickness decreases more with height on stems of fire-resistant than fire-sensitive Floridian oaks (Quercus spp.; Fagaceae). *American Journal of Botany* 101:2183–2188.

Hoffmann WA, Geiger EL, Gotsch SG, Rossatto DR, Silva LCR, Lau OL, Haridasan M, Franco AC. 2012. Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters* 15:759–768.

Klimešová J, Klimeš L. 2007. Bud banks and their role in vegetative regeneration – A literature review and proposal for simple classification and assessment. *Perspectives in Plant Ecology* 8:115–129.

Lamont BB, He T, Yan Z. 2019. Evolutionary history of fire-stimulated resprouting, flowering, seed release and germination. *Biological Reviews* 94:903–928.

Lawes MJ, Midgley JJ, Clarke PJ. 2013. Costs and benefits of relative bark thickness in relation to fire damage: a savanna/forest contrast. *Journal of Ecology* 101:517–524.

Lawes MJ, Woolley L, Van Holsbeeck S, Murphy BP, Burrows GE, Midgley JJ. 2021. Bark functional ecology and its influence on the distribution of Australian half-butt eucalypts. *Austral Ecology* 46:1097–1111.

Loram-Lourenço L, Farnese F dos S, Sousa LF de, Alves RDFB, Andrade MCP de, Almeida SE da S, Moura LM de F, Costa AC, Silva FG, Galmés J, Cochard H, Franco AC, Menezes-Silva PE. 2020. A Structure Shaped by Fire, but Also Water: Ecological Consequences of the Variability in Bark Properties Across 31 Species From the Brazilian Cerrado. *Frontiers in Plant Sciences* 10:1718.

MacArthur RH. 1961. Population Effects of Natural Selection. *The American Naturalist* 95:195–199.

Melo ACG, Durigan G. 2009. *Plano de Manejo - Estação Ecológica de Santa Bárbara* (Resumo Executivo). Instituto Florestal, Secretaria do Meio Ambiente.

Ott JP, Klimešová J, Hartnett DC. 2019. The ecology and significance of below-ground bud banks in plants. *Annals of Botany* 123:1099–1118.

Pausas JG. 2015a. Alternative fire-driven vegetation states. *Journal of Vegetation Science* 26:4–6.

Pausas JG. 2015b. Bark thickness and fire regime. *Functional Ecology* 29:315–327.

Pausas JG, Lamont BB, Paula S, Appezzato-da-Glória B, Fidelis A. 2018. Unearthing belowground bud banks in fire-prone ecosystems. *New Phytologist* 217:1435–1448.

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.

R Core Team (2022) R system version 4.3.1.

Richards CL, Muth NZ, Pigliucci M. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* 9:981–993.

Rodrigues CA, Zirondi HL, Fidelis A. 2021. Fire frequency affects fire behavior in open savannas of the Cerrado. *Forest Ecology and Management* 482:118850.

Rosell JA, Gleason S, Méndez-Alonzo R, Chang Y, Westoby M. 2014. Bark functional ecology: evidence for tradeoffs, functional coordination, and environment producing bark diversity. *New Phytologist* 201:486–497.

Rosell JA, Piper FI, Jiménez-Vera C, Vergílio PCB, Marcati CR, Castorena M, Olson ME. 2021. Inner bark as a crucial tissue for non-structural carbohydrate storage across three tropical woody plant communities. *Plant, Cell & Environment* 44:156–170.

Rossatto DR, Hoffmann WA, Franco AC. 2009. Differences in growth patterns between co-occurring forest and savanna trees affect the forest-savanna boundary. *Functional Ecology* 23:689–698.

Scalon MC, Domingos FMCB, da Cruz WJA, Marimon-Junior BH, Marimon BS, Oliveras I. 2020. Diversity of functional trade-offs enhances survival after fire in Neotropical savanna species. *Journal of Vegetation Science* 31:139–150.

Scalon MC, Rossatto DR, Oliveras I, Miatto RC, Gray EF, Domingos FMCB, Brum FT, Carlucci MB, Hoffmann WA, Marimon-Júnior BH, Marimon BS, Franco AC. 2021. Fire and drought: Shifts in bark investment across a broad geographical scale for Neotropical savanna trees. *Basic and Applied Ecology* 56:110–121.

Schafer JL, Breslow BP, Hohmann MG, Hoffmann WA. 2015. Relative Bark Thickness is Correlated with Tree Species Distributions along a Fire Frequency Gradient. *Fire Ecology* 11:74–87.

Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9:671–675.

Staver AC, Archibald S, Levin SA. 2011. The Global Extent and Determinants of Savanna and Forest as Alternative Biome States. *Science* 334:230–232.

VanderWeide BL, Hartnett DC. 2011. Fire resistance of tree species explains historical gallery forest community composition. *Forest Ecology and Management* 261:1530–1538.

Wigley BJ, Charles-Dominique T, Hempson GP, Stevens N, TeBeest M, Archibald S, Bond WJ, Bunney K, Coetsee C, Donaldson J, Fidelis A, Gao X, Gignoux J, Lehmann C, Massad TJ, Midgley JJ, Millan M, Schwilk D, Siebert F, Solofondranohatra C, Staver AC, Zhou Y, Kruger LM. 2020. A handbook for the standardised sampling of plant functional traits in disturbance-prone ecosystems, with a focus on open ecosystems. *Australian Journal of Botany*.

Zupo T, Daibes LF, Pausas JG, Fidelis A. 2021. Post-fire regeneration strategies in a frequently burned Cerrado community. Journal of Vegetation Science 32.

List of captions to the figures:

Figure 1. Examples of vegetation types sampled in this study, aerial view. **a)** open savanna **b)** woody savanna **c)** cerradão **d)** seasonal semi-deciduous forest. Photos by Dhemerson Conciani.

Figure 2. Bud and bark traits evaluated in savanna and forest species across a fire frequency gradient. **(a)** Schematic illustration of levels of bud protection and method for measuring bark growth rate. The longitudinal section shows levels of bud protection (I_{BP}0 = buds fully exposed; 1 = buds exposed but with their meristems protected; 2 = buds in bark depressions; 3 = buds fully covered by bark). The transversal section shows stem variables recorded for the calculation of bark growth rate. **(b)** Examples of stem anatomy of woody species (with their corresponding I_{BP}). Species ranked from lower to higher bud protection are: *Tapirira guianensis* (Anacardiaceae), *Moquiniastrum polymorphum* (Asteraceae), *Stryphnodendron rotundifolium* (Fabaceae), and *Aspidosperma tomentosum* (Apocynaceae).

Figure 3. Dispersion of 123 Cerrado species according to their area of occurrence and their bark growth rate. Species were separated into specialists or generalists (when they inhabit at least one savanna and one forest area) and into trees and shrubs. The dashed horizontal line shows the threshold below which most individuals get filtered out by fire in savanna. Boxplots represent the bark growth rate in **a)** each vegetation according to the whole community and **b)** to the species' growth form. Species within the lower dark-gray rectangle produce bark lower than the threshold, while species above the dashed line produce bark higher than the threshold. Variation in bark production of generalist species sampled in both forests and savannas is shown in **c**. The dashed lines represent the mean bark growth of generalist species in forests (teal) and savannas (orange).

Tables

Table 1 Bark growth rate (BGR, mm/growth units^{-1}, mean±SD) across species and communities from different vegetation types (open and woody savannas or cerradão and semi-deciduous forests), exposed to different amounts of fire events and with different degrees of bud protection. The index of bud protection ranges from 0 to 3, where 0 corresponds to an unprotected bud and 3 is a bud fully covered by bark. Letters indicate significant differences ($P \leq 0.05$) in the pairwise post-hoc test between vegetation types, according to bud protection level and fire frequency. CWM = community-weighted means for BGR.

Vegetation type	**Species BGR**
open savanna	0.37 ± 0.27 a
woody savanna	0.27 ± 0.21 a
cerradão	0.15 ± 0.11 b
semi-deciduous forest	0.05 ± 0.09 b
Bud protection (I_{BP})	
0	0.14 ± 0.13 a
1	0.18 ± 0.16 a
2	0.42 ± 0.23 b
3	0.54 ± 0.24 b
Fire frequency	**CWM BGR**
none (0 events)	0.107 a
low (1-2 events)	0.293 b
high (5-9 events)	0.379 b