



**HAL**  
open science

## 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-04047093>**

Submitted on 24 Oct 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 Original Article

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

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

5 Marco Chiminazzo<sup>1\*</sup>, Aline Bertolosi Bombo<sup>1</sup>, Tristan Charles-Dominique<sup>2,3</sup>, Alessandra  
6 Fidelis<sup>1</sup>

7 <sup>1</sup> Lab of Vegetation Ecology, Universidade Estadual Paulista (UNESP), Instituto de  
8 Biociências, Avenida 24-A, 1515, Rio Claro, 13506-900, Brazil.

9 <sup>2</sup> AMAP, Univ Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France.

10 <sup>3</sup> Institute of Ecology and Environmental Sciences – Paris CNRS UMR 7618, Sorbonne  
11 University, Paris, France.

12

13

14 **Author for correspondence:** Marco Chiminazzo

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

17

18

19

20

21

22

23

24

## 1      **Summary**

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

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

4  
5   **Keywords:** bark growth rate, bark thickness, bud protection, fire, savanna-forest boundaries,  
6   neotropical savannas, persistence niche, resprouting.

7

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

24

25

26

27

## 1 INTRODUCTION

2 Savannas have a continuous flammable grass layer that supports frequent fires, creating a  
3 harsh environment for trees to persist as their aboveground parts are exposed to flames  
4 (Bond, 2013). In contrast, forests present a continuous tree canopy, which shades out  
5 flammable grasses (Hoffmann et al., 2012; Charles-Dominique et al., 2018). Tropical  
6 savannas and forests are distributed in mosaics mostly maintained by fire (Staver et al., 2011;  
7 Pausas, 2015a), which selects species capable of persisting in fire-prone ecosystems  
8 (Rossatto et al., 2009; Hoffmann et al., 2012; Charles-Dominique et al., 2015a; Lamont et al.,  
9 2019). Bark thickness of woody species is a key trait that enables their survival during fires  
10 by protecting the inner tissues of the stem from the flames and the heat (Lawes et al., 2013;  
11 Rosell et al., 2014; Pausas, 2015b), thus allowing the species to resprout new branches from  
12 their aerial buds (Bond and Midgley, 2001; Clarke et al., 2013).

13         Bark tissues are responsible for providing mechanical and chemical protection to the  
14 plant inner living tissues and to meristematic regions responsible for the plant regeneration  
15 (Burrows, 2002; VanderWeide and Hartnett, 2011; Hoffmann et al., 2012; Schafer et al.,  
16 2015; Scalon et al., 2020). Bark is not only important for insulating vital tissues, but also for  
17 storing important resources like nonstructural carbohydrates which are fundamental for  
18 resprouting post-fire (Clarke et al., 2013; Rosell et al., 2021). In fire-prone ecosystems, the  
19 rate at which bark is produced (*bark growth rate* hereafter) is crucial for species persistence,  
20 as it determines their capacity to accumulate enough bark between fire events (VanderWeide  
21 and Hartnett, 2011; Schafer et al., 2015; Charles-Dominique et al., 2017; Wigley et al., 2020).

22         In flammable ecosystems, woody plants are expected either to prioritize a fast vertical  
23 growth when fires are less frequent and less intense (Lanky strategy) or to prioritize a fast  
24 bark growth rate when fire is more frequent and intense (Corky strategy; Dantas and Pausas,

1 2013). Neotropical savannas are largely dominated by plants with the Corky strategy, thus  
2 accounting for a greater bark investment when compared to Afrotropical savanna woody  
3 species (Dantas and Pausas, 2013). However, different growth forms - like trees and shrubs -  
4 coexist in those areas. This coexistence is puzzling: while trees can grow their canopy above  
5 the flame height and escape the firetrap, shrubs complete all their developmental stages  
6 within the flame zone due to their lower stature. These differences suggest that low and high  
7 statured plants (i.e., shrubs and trees) would require very different rates of bark production  
8 with strong implications over their allocation strategies.

9         In frequently disturbed environments, the fitness of plants can depend much more on  
10 surviving in early stages than outcompeting neighbors or reproducing abundantly (Bond and  
11 Midgley, 2001); with species often relying in bud protection and bark production to persist in  
12 the environment (Clarke et al., 2013; Pausas, 2015b; Pausas et al., 2018). Previous  
13 investigations in African savannas revealed that bark growth rate and bud protection are not  
14 strongly correlated, suggesting that buds are not simply passively buried under bark but  
15 instead maintained actively in or out the bark layer over time (Charles-Dominique et al.,  
16 2017). Further, the two traits could be expressed in combination to promote fire resistance  
17 and to enhance resprouting capacity. As these first observations were made in African  
18 vegetation that faces less intense fires than the Cerrado (a species-rich, tropical savanna  
19 located in Brazil, where fire is one of the major drivers maintaining the mosaics of savannas  
20 and forests; Dantas and Pausas, 2013; Charles-Dominique et al., 2017), here we investigate  
21 whether these two traits (aerial bud protection and bark growth rate) are more frequently  
22 combined in neotropical species exposed to more intense grass fires than those from the  
23 Afrotropical savannas.

24         Although woody communities from savannas and forests differ in composition and  
25 structure, some species can inhabit both environments (generalists). We distinguish them

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

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

24  
25 **MATERIALS AND METHODS**

## 1 ***Study area***

2 We conducted the study at the Santa Bárbara Ecological Station (SBES, 22°48'59'' S,  
3 49°14'12'' W, 589 m.a.s.l.), a protected area in southeastern Brazil that comprises a wide  
4 diversity of co-existing vegetation types. Mean temperature ranges from 18 to 22 °C and  
5 mean annual rainfall from 1,000 to 1,300 (Melo and Durigan, 2009). Climate is seasonal,  
6 with a wet and hot summer and a dry and mild winter. We selected four different vegetation  
7 types with contrasted fire frequencies (fire events calculated over from 1984 to 2018;  
8 Conciani et al, 2021): i) *open savannas*, high fire frequency with 5-9 fire events; defined by  
9 high grass cover (up to 80%) co-occurring with short trees and scattered shrubs; ii) *woody*  
10 *savannas*, low fire frequency with 0-2 fire events; characterized by a lower grass cover (up to  
11 50%) and taller trees capable of suppressing the continuous grass layer by shading locally; iii)  
12 *cerradão*, no fire event; forests composed of a mix of generalists (species occurring in both  
13 savannas and forests) and dry forest species; and iv) *seasonal semi-deciduous forest*, no fire  
14 event; forests composed of tall tree species of the Atlantic Rainforest (Fig. 1, Coutinho,  
15 1990).

## 16 17 ***Sampling design and study species***

18 We randomly established 10 transects of 10 x 40 m in each vegetation type. We registered  
19 every woody individual with a height between 1.5 and 3 m, because within this height  
20 different growth forms (trees and shrubs) are exposed to the flames, thus creating a  
21 bottleneck that woody species must overcome to persist in the environment. For each  
22 sampled species within the transects, we collected three to five branches from three different  
23 individuals in every vegetation type they occurred and scored the predominant growth form  
24 according to Abreu et al. (2017) and Flora do Brasil (2020). We then classified every species  
25 as savanna exclusive, forest exclusive, or generalists (species that inhabits at least one



1 savanna and one forest vegetation) according to Abreu et al. (2017) and Flora do Brasil  
2 (2020). To compare the bark production of generalist species growing into forests and  
3 savannas, we analyzed ten different species that were sampled in at least one savanna and one  
4 forest in our study area: *Copaifera langsdorffii* Desf. (Fabaceae), *Erythroxylum pelleterianum*  
5 A.St.-Hil. (Erythroxylaceae), *Luehea grandiflora* Mart. & Zucc. (Malvaceae), *Moquiniastrum*  
6 *polymorphum* (Less.) G. Sancho (Asteraceae), *Myrcia multiflora* (Lam.) DC. (Myrtaceae),  
7 *Pera glabrata* (Schott) Baill. (Peraceae), *Tabernaemontana hystrix* Steud. (Apocynaceae),  
8 *Terminalia glabrescens* Mart. (Combretaceae), *Trichilia pallida* Sw. (Meliaceae) and  
9 *Vochysia tucanorum* Mart. (Vochysiaceae).

10

### 11 ***Trait description***

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

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

18

### 19 *Statistical analyses*

20 We used generalized linear mixed effect models (GLMM) to analyze how bark growth rate  
21 was distributed across vegetation types with different fire frequencies and between species'  
22 growth forms (shrubs and trees). We considered sampled individuals as a random effect and  
23 the vegetation type and growth form as fixed effects. After testing the significance of fixed  
24 effects, we performed pairwise comparisons using post hoc tests of Tuckey type with  
25 Bonferroni correction. We used generalized linear models (GLM) to analyze the relationship

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

## 19 20 **RESULTS**

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

1 < 0.01, Fig. 3c). No interaction was detected between bark growth rate of different growth  
2 forms and among the similar vegetation types (open/woody savanna and cerrado/semi-  
3 deciduous forests). Contrary to our predictions, the bark production of trees and shrubs did  
4 not differ. However, within each vegetation type, trees showed a tendency of producing more  
5 bark than shrubs (Fig. 3b). Species BGR scores are shown in Supplementary Information  
6 (Table S1).

7 Community-weighted means (CWM) for bark growth rate varied according to fire  
8 frequency (Table 1). Savannas with high fire frequency (*open savannas*, 5-9 fire events) had  
9 CWM values of bark growth rate of 0.379 mm/year, while savannas with lower fire  
10 frequency (*woody savannas*, 1-2 fire events) showed a CWM of 0.293 mm/year. Forest  
11 systems (no fire) showed a CWM of 0.107 mm/year. A shift from forest to savanna  
12 communities was found at the first quartile ranking species' bark production in open  
13 savannas and the third quartile in the semi-deciduous forest, indicating that a minimum bark  
14 growth rate of *c.* 0.13 mm/year is required for species to occur in fire-prone systems (Fig. 3),  
15 thus differentiating communities of forests and savannas ( $P \leq 0.001$ , Table 1). Above this  
16 threshold, most species occurring in open (33 species, 80% of the community) and woody (40  
17 species, 71%) savannas produce at least 0.13 mm of bark. In forests, only 20 (41%) species  
18 from the cerrado and 6 (18%) species from the semi-deciduous forest produced more than  
19 0.13 mm of bark. Out of the 26 species sampled in forest that produced bark above this  
20 threshold, 30% are forest specialists, 38% are generalists, and 26% are savanna specialists (in  
21 forests, these savanna-specialist species were represented by one or two individuals and were  
22 sampled in the cerrado). In savannas, out of the 25 sampled species that produced bark  
23 below the threshold, 32% are generalists and 59% are savanna specialists (we did not account  
24 species without available information about their habitat of preference and one forest  
25 specialist species sampled in the open savanna; Fig. 3a). The ratio between wood growth rate

1 and bark growth rate differed greatly across vegetation types ( $P \leq 0.001$ ) and between  
2 generalists and specialists ( $P \leq 0.01$ ; Fig. S1, Table S2), thus indicating that allocation to bark  
3 differed. Lastly, woody individuals with higher degrees of bud protection ( $I_{BP} = 2, 3$ )  
4 produced bark *c.* 2 times faster than individuals with low or no bud protection ( $I_{BP} = 0, 1$ ;  
5 Table 1,  $P \leq 0.001$ ).

## 6 7 **DISCUSSION**

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

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

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

20 When fire is suppressed from savannas, generalist species are usually those  
21 contributing the most to the density of woody communities (Flake et al., 2021). These species  
22 can produce bark above the threshold at an equal rate as many savanna-specialist species and  
23 could develop in savannas where fire is present. Interestingly, generalist species sampled in  
24 forests where fire is absent have bark production that is equivalent to forest specialists. This

1 capacity of generalist species to adjust their bark production according to their environment  
2 defines them as “jack-of-all-trades-mater-of-some”, a strategy that characterizes the most  
3 ecologically successful species, such as invasive ones (see Richards et al., 2006). Further  
4 studies should focus on the physiological mechanisms explaining this ability to adjust bark  
5 production and the associated benefits in terms of cost reduction and increased survival as  
6 generalists could have a profound effect on forest-savanna mosaics by allowing transitions  
7 between them and induce successional patterns that are not simply driven by increasing  
8 shade. Importantly, further investigation could help understand how this bark adjustment is  
9 performed by the plant and how it relates to the overall allocation strategies.

10

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

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

1           Out of the few species inhabiting savannas and producing bark below the threshold,  
2 most of them are shrubs (66%) and savanna specialists (54%), thus suggesting the presence  
3 of alternative strategies for shrub persistence in savannas. Strategies other than investing in  
4 bark production aboveground, like trichomes covering buds (Chiminazzo et al., 2021) and  
5 resprouting from belowground bud-bearing organs were reported for most of these species  
6 (Pilon et al., 2021; Zupo et al., 2021; Chiminazzo et al., 2021). Therefore, although bark  
7 production is strongly linked to savanna communities, shrub species can trade this strategy by  
8 allocating most of their biomass belowground – also allowing them to persist in the post-fire  
9 environment (Klimešová and Klimeš, 2007, Pausas et al., 2018; Ott et al., 2019; Pilon et al.,  
10 2021; Zupo et al., 2021; Chiminazzo et al., 2021). Hence, bark production alone cannot fully  
11 explain the assembly of communities with different growth forms in fire-prone ecosystems.

12

### 13 *A greater bark production accounts for a better aerial bud protection*

14           Our results indicate that bark growth rate was strongly related to bud protection.  
15 Previous examples on Afrotropical savannas showed that bud protection was only weakly  
16 correlated to bark production (Charles-Dominique et al., 2017). A possible reason for these  
17 divergences may be differences in fire frequencies and intensities, since the Cerrado is  
18 exposed to more intense fires than the Afrotropical savannas (Dantas and Pausas, 2013).  
19 However, differences in fire intensities/frequencies may not fully explain the bark  
20 production-bud protection relationship: conifers exposed to surface fires (e.g., in the Andes  
21 and the western North America) can produce thick bark capable of surviving fires (Pausas,  
22 2015b), but this group of plants can present empty axils and meristems embedded near the  
23 bark surface translating into a lower bud protection (Burrows et al., 2003). Conversely,  
24 eucalypts are remarkable for expressing the highest bud protection (embedded within the



1 wood) while having very low bark thickness (Burrows, 2002). The relationship between bark  
2 production and aerial bud protection should therefore be investigated more widely across  
3 different systems and species clades to better understand the ecological meanings of either  
4 investing in bud protection, or in greater bark growth rate, or in both.

## 5 *Conclusions*

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

15

## 16 **ACKNOWLEDGMENTS**

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

22

## 23 **FUNDING**

24 This study was supported by FAPESP (2015/06743-0) and CNPq (406505/2018-7). MAC  
25 received financial support from CNPq (134582/2018-7) and FAPESP (2018/21300-6,

1 2021/09269-9), ABB from FAPESP (2017/02934-1) and AF received grant from CNPq  
 2 (312689/2021). This study was authorized by the COTEC N. 57/2019 D144/2018 PH.

3  
 4  
 5

## 5 REFERENCES

- 6 Abreu RCR, Hoffmann WA, Vasconcelos HL, Pilon NA, Rossatto DR, Durigan G. 2017. The  
 7 biodiversity cost of carbon sequestration in tropical savanna. *Science Advances*  
 8 3:e1701284.
- 9 Barthélémy D, Caraglio Y. 2007. Plant Architecture: A Dynamic, Multilevel and  
 10 Comprehensive Approach to Plant Form, Structure and Ontogeny. *Annals of Botany*  
 11 99:375–407.
- 12 Bond WJ. 2013. *Fire and plants*. London: Chapman & Hall.
- 13 Bond WJ, Midgley JJ. 2001. Ecology of sprouting in woody plants: the persistence niche.  
 14 *Trends in Ecology and Evolution* 16:45–51.
- 15 Burrows GE. 2002. Epicormic strand structure in Angophora, Eucalyptus and Lophostemon  
 16 (Myrtaceae) - implications for fire resistance and recovery. *New Phytologist* 153:111–  
 17 131.
- 18 Burrows GE, Offord CA, Meagher PF, Ashton K. 2003. Axillary Meristems and the  
 19 Development of Epicormic Buds in Wollemi Pine (*Wollemia nobilis*). *Annals of*  
 20 *Botany* 92:835–844.
- 21 Charles-Dominique T, Beckett H, Midgley GF, Bond WJ. 2015a. Bud protection: a key trait  
 22 for species sorting in a forest-savanna mosaic. *New Phytologist* 207:1052–1060.
- 23 Charles-Dominique T, Midgley GF, Bond WJ. 2017. Fire frequency filters species by bark  
 24 traits in a savanna-forest mosaic. *Journal of Vegetation Science* 28:728–735.
- 25 Charles-Dominique T, Midgley GF, Tomlinson KW, Bond WJ. 2018. Steal the light: shade  
 26 vs fire adapted vegetation in forest-savanna mosaics. *New Phytologist* 218:1419–  
 27 1429.
- 28 Charles-Dominique T, Staver AC, Midgley GF, Bond WJ. 2015b. Functional differentiation  
 29 of biomes in an African savanna/forest mosaic. *South African Journal of Botany*  
 30 101:82–90.
- 31 Chiminazzo MA, Bombo AB, Charles-Dominique T, Fidelis A. 2021. Your best buds are  
 32 worth protecting: Variation in bud protection in a fire-prone cerrado system.  
 33 *Functional Ecology* 35:2424–2434.
- 34 Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox  
 35 KJE. 2013. Resprouting as a key functional trait: how buds, protection and resources  
 36 drive persistence after fire. *New Phytologist* 197:19–35.
- 37 Conciani DE, Santos LP dos, Silva TSF, Durigan G, Alvarado ST. 2021. Human-climate  
 38 interactions shape fire regimes in the Cerrado of São Paulo state, Brazil. *Journal for*  
 39 *Nature Conservation* 61:126006.
- 40 Coutinho LM. 1990. Fire in the Ecology of the Brazilian Cerrado. *Fire in the Tropical Biota*.  
 41 Ecological Studies, Goldammer JG (ed) Springer Berlin Heidelberg, Berlin,  
 42 Heidelberg, p 82–105
- 43 Dantas V de L, Batalha MA, Pausas JG. 2013. Fire drives functional thresholds on the  
 44 savanna–forest transition. *Ecology* 94:2454–2463.
- 45 Dantas V de L, Pausas JG. 2013. The lanky and the corky: fire-escape strategies in savanna  
 46 woody species. *Journal of Ecology* 101:1265–1272.

- 1 Flake SW, Abreu RCR, Durigan G, Hoffmann WA. 2021. Savannas are not old fields:  
2 Functional trajectories of forest expansion in a fire-suppressed Brazilian savanna are  
3 driven by habitat generalists. *Functional Ecology* 35:1797–1809.
- 4 Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro. Available at  
5 <<http://floradobrasil.jbrj.gov.br>>. Accessed on 06 Jan. 2023.
- 6 Futuyma DJ, Moreno G. 1988. The Evolution of Ecological Specialization. *Annual Review of*  
7 *Ecology, Evolution and Systematics* 19:207–233.
- 8 Graves SJ, Rifai SW, Putz FE. 2014. Outer bark thickness decreases more with height on  
9 stems of fire-resistant than fire-sensitive Floridian oaks (*Quercus* spp.; Fagaceae).  
10 *American Journal of Botany* 101:2183–2188.
- 11 Hoffmann WA, Geiger EL, Gotsch SG, Rossatto DR, Silva LCR, Lau OL, Haridasan M,  
12 Franco AC. 2012. Ecological thresholds at the savanna-forest boundary: how plant  
13 traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters*  
14 15:759–768.
- 15 Klimešová J, Klimeš L. 2007. Bud banks and their role in vegetative regeneration – A  
16 literature review and proposal for simple classification and assessment. *Perspectives*  
17 *in Plant Ecology* 8:115–129.
- 18 Lamont BB, He T, Yan Z. 2019. Evolutionary history of fire-stimulated resprouting,  
19 flowering, seed release and germination. *Biological Reviews* 94:903–928.
- 20 Lawes MJ, Midgley JJ, Clarke PJ. 2013. Costs and benefits of relative bark thickness in  
21 relation to fire damage: a savanna/forest contrast. *Journal of Ecology* 101:517–524.
- 22 Lawes MJ, Woolley L, Van Holsbeeck S, Murphy BP, Burrows GE, Midgley JJ. 2021. Bark  
23 functional ecology and its influence on the distribution of Australian half-butt  
24 eucalypts. *Austral Ecology* 46:1097–1111.
- 25 Loram-Lourenço L, Farnese F dos S, Sousa LF de, Alves RDFB, Andrade MCP de, Almeida  
26 SE da S, Moura LM de F, Costa AC, Silva FG, Galmés J, Cochard H, Franco AC,  
27 Menezes-Silva PE. 2020. A Structure Shaped by Fire, but Also Water: Ecological  
28 Consequences of the Variability in Bark Properties Across 31 Species From the  
29 Brazilian Cerrado. *Frontiers in Plant Sciences* 10:1718.
- 30 MacArthur RH. 1961. Population Effects of Natural Selection. *The American Naturalist*  
31 95:195–199.
- 32 Melo ACG, Durigan G. 2009. *Plano de Manejo - Estação Ecológica de Santa Bárbara*  
33 (Resumo Executivo). Instituto Florestal, Secretaria do Meio Ambiente.
- 34 Ott JP, Klimešová J, Hartnett DC. 2019. The ecology and significance of below-ground bud  
35 banks in plants. *Annals of Botany* 123:1099–1118.
- 36 Pausas JG. 2015a. Alternative fire-driven vegetation states. *Journal of Vegetation Science*  
37 26:4–6.
- 38 Pausas JG. 2015b. Bark thickness and fire regime. *Functional Ecology* 29:315–327.
- 39 Pausas JG, Lamont BB, Paula S, Appezzato-da-Glória B, Fidelis A. 2018. Unearthing  
40 belowground bud banks in fire-prone ecosystems. *New Phytologist* 217:1435–1448.
- 41 Pilon NAL, Cava MGB, Hoffmann WA, Abreu RCR, Fidelis A, Durigan G. 2021. The  
42 diversity of post-fire regeneration strategies in the cerrado ground layer. *Journal of*  
43 *Ecology* 109:154–166.
- 44 R Core Team (2022) R system version 4.3.1.
- 45 Richards CL, Muth NZ, Pigliucci M. 2006. Jack of all trades, master of some? On the role of  
46 phenotypic plasticity in plant invasions. *Ecology Letters* 9:981–993.
- 47 Rodrigues CA, Zironi HL, Fidelis A. 2021. Fire frequency affects fire behavior in open  
48 savannas of the Cerrado. *Forest Ecology and Management* 482:118850.

- 1 Rosell JA, Gleason S, Méndez-Alonzo R, Chang Y, Westoby M. 2014. Bark functional  
2 ecology: evidence for tradeoffs, functional coordination, and environment producing  
3 bark diversity. *New Phytologist* 201:486–497.
- 4 Rosell JA, Piper FI, Jiménez-Vera C, Vergilio PCB, Marcati CR, Castorena M, Olson ME.  
5 2021. Inner bark as a crucial tissue for non-structural carbohydrate storage across  
6 three tropical woody plant communities. *Plant, Cell & Environment* 44:156–170.
- 7 Rossatto DR, Hoffmann WA, Franco AC. 2009. Differences in growth patterns between co-  
8 occurring forest and savanna trees affect the forest-savanna boundary. *Functional  
9 Ecology* 23:689–698.
- 10 Scalon MC, Domingos FMCB, da Cruz WJA, Marimon-Junior BH, Marimon BS, Oliveras I.  
11 2020. Diversity of functional trade-offs enhances survival after fire in Neotropical  
12 savanna species. *Journal of Vegetation Science* 31:139–150.
- 13 Scalon MC, Rossatto DR, Oliveras I, Miatto RC, Gray EF, Domingos FMCB, Brum FT,  
14 Carlucci MB, Hoffmann WA, Marimon-Júnior BH, Marimon BS, Franco AC. 2021.  
15 Fire and drought: Shifts in bark investment across a broad geographical scale for  
16 Neotropical savanna trees. *Basic and Applied Ecology* 56:110–121.
- 17 Schafer JL, Breslow BP, Hohmann MG, Hoffmann WA. 2015. Relative Bark Thickness is  
18 Correlated with Tree Species Distributions along a Fire Frequency Gradient. *Fire  
19 Ecology* 11:74–87.
- 20 Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image  
21 analysis. *Nature Methods* 9:671–675.
- 22 Staver AC, Archibald S, Levin SA. 2011. The Global Extent and Determinants of Savanna  
23 and Forest as Alternative Biome States. *Science* 334:230–232.
- 24 VanderWeide BL, Hartnett DC. 2011. Fire resistance of tree species explains historical  
25 gallery forest community composition. *Forest Ecology and Management* 261:1530–  
26 1538.
- 27 Wigley BJ, Charles-Dominique T, Hempson GP, Stevens N, TeBeest M, Archibald S, Bond  
28 WJ, Bunney K, Coetsee C, Donaldson J, Fidelis A, Gao X, Gignoux J, Lehmann C,  
29 Massad TJ, Midgley JJ, Millan M, Schwilk D, Siebert F, Solofondranohatra C, Staver  
30 AC, Zhou Y, Kruger LM. 2020. A handbook for the standardised sampling of plant  
31 functional traits in disturbance-prone ecosystems, with a focus on open ecosystems.  
32 *Australian Journal of Botany*.
- 33 Zupo T, Daibes LF, Pausas JG, Fidelis A. 2021. Post-fire regeneration strategies in a  
34 frequently burned Cerrado community. *Journal of Vegetation Science* 32.

37 **List of captions to the figures:**

38

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

42

1 **Figure 2.** Bud and bark traits evaluated in savanna and forest species across a fire frequency  
 2 gradient. **(a)** Schematic illustration of levels of bud protection and method for measuring bark  
 3 growth rate. The longitudinal section shows levels of bud protection ( $I_{BP}0$  = buds fully  
 4 exposed; 1 = buds exposed but with their meristems protected; 2 = buds in bark depressions;  
 5 3 = buds fully covered by bark). The transversal section shows stem variables recorded for  
 6 the calculation of bark growth rate. **(b)** Examples of stem anatomy of woody species (with  
 7 their corresponding  $I_{BP}$ ). Species ranked from lower to higher bud protection are: *Tapirira*  
 8 *guianensis* (Anacardiaceae), *Moquiniastrum polymorphum* (Asteraceae), *Stryphnodendron*  
 9 *rotundifolium* (Fabaceae), and *Aspidosperma tomentosum* (Apocynaceae).

10

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

## 21 **Tables**

22 **Table 1** Bark growth rate (BGR, mm/growth units<sup>-1</sup>, mean±SD) across species and  
 23 communities from different vegetation types (open and woody savannas or cerradão and  
 24 semi-deciduous forests), exposed to different amounts of fire events and with different  
 25 degrees of bud protection. The index of bud protection ranges from 0 to 3, where 0

1 corresponds to an unprotected bud and 3 is a bud fully covered by bark. Letters indicate  
 2 significant differences ( $P \leq 0.05$ ) in the pairwise post-hoc test between vegetation types,  
 3 according to bud protection level and fire frequency. CWM = community-weighted means  
 4 for BGR.

<b>Vegetation type</b>	<b>Species BGR</b>
open savanna	$0.37 \pm 0.27$ a
woody savanna	$0.27 \pm 0.21$ a
cerradão	$0.15 \pm 0.11$ b
semi-deciduous forest	$0.05 \pm 0.09$ b

  

<b>Bud protection (<math>I_{BP}</math>)</b>	
0	$0.14 \pm 0.13$ a
1	$0.18 \pm 0.16$ a
2	$0.42 \pm 0.23$ b
3	$0.54 \pm 0.24$ b

  

<b>Fire frequency</b>	<b>CWM BGR</b>
none (0 events)	0.107 a
low (1-2 events)	0.293 b
high (5-9 events)	0.379 b

5