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Fire and drought: Shifts in bark investment across a broad geographical scale for Neotropical savanna trees

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Abstract

Savanna tree communities occurring in confluence zones with other biomes likely experience different environmental pressures, resulting in shifts in the selection of individual traits, the combinations of such traits, and species composition. In seasonally dry fire-prone environments, plant survival is presumably associated with adaptive changes in bark properties related to fire protection and water storage. Here, we integrated the multiple functions of the bark to investigate whether different selective pressures could influence patterns of variation in bark structure and allocation across species in a broad geographical range. We measured thickness, density, and water content of the inner and outer bark in branches and the main stem of the 51 most abundant species in three savanna communities differing in climatic aridity, one located at the core region of Cerrado in Central Brazil and the other two at its periphery, in the transition zones with Amazonia and Atlantic forest biomes. We found no difference in outer bark thickness but markedly difference in inner bark thickness between the three plant communities. In the central region, where dry season is long and fire is frequent, branches and main stem showed thicker inner bark. Contrastingly, in the

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south periphery region, where dry season is short, species showed thinner inner bark in both branches and main stem. Species from the north periphery region, where mean annual precipitation is higher, but fire is frequent and the dry season is also long, showed similar main stem inner bark thickness, but thinner branch inner bark compared to core region species. Our findings support the idea that investing in inner bark thickness and bark moisture may be the most advantageous strategy in plant communities that suffer from high evaporative demand during a long period and are at a high risk of fire.

Keywords: bark; biome transition; Cerrado; fire ecology; phellogen; water storage

Introduction

Transition zones located at the confluence of different biomes have a more dynamic nature compared to regions that are further away from the biomes boundaries (Costa et al., 2018; Marimon et al., 2014). In addition, these areas will likely be the most affected regions under future climate change scenarios (Gosz, 1992; Marimon et al., 2014). Distinct environmental drivers acting in these different regions influence plant community turnover within the biome range (Neves et al., 2017), the functional responses of different assemblages to the prevailing environmental conditions (Risser, 1995), and their recovery patterns from perturbations (Dantas, Hirota, Oliveira, & Pausas, 2016; Risser, 1995). Various hypotheses have been proposed to explain the observed patterns of within-biome beta diversity across multiple taxa (Risser, 1995). Because biome transitions are also major breaks in the distribution of many species (Gosz, 1992), and the core regions usually harbour higher species richness (van der Maarel, 1990), it can be expected that the core regions will have higher functional diversity, since species richness and functional diversity can be positively correlated (Petchey & Gaston 2002). On the other hand, greater species richness might be observed in transition zones because local assemblages might be enriched with taxa from the adjacent biomes (Risser, 1995), and the higher environmental instability of the biome periphery can also maintain higher richness levels (Stein, Gerstner, & Kreft, 2014). In this later case, both processes will favour higher functional trait diversity in the biome periphery (Mayfield et al., 2010). Nevertheless, irrespective of the considered scenario, predictions suggest that plant functional traits at the community level will vary between core and periphery regions of a biome, and that this variation will also result in a different selection of trait combinations and species in these different regions (Reu et al., 2011).

Located in Central Brazil, the Neotropical Brazilian Savanna (known as Cerrado) had originally continental proportions (2.0×10^6 km^2) within a wide latitudinal range (2° to 24°S) and is under the influence of different biomes at its boundaries, such as the closed-canopy Amazon Forest in the north and the Atlantic Forest in the south (IBGE, 2004, Fig. 1). Open savanna woodland (i.e., typical cerrado) is the predominant vegetation type, which thrives in a region characterized by strong rainfall seasonality and drying of the upper soil layers during the dry season, high atmospheric evaporative demand, nutrient-poor soils and frequent fires (Castro, Martins, Tamashiro, & Shepherd, 1999; Eiten, 1972). The whole biome experiences strong rainfall seasonality, with most of the rains occurring during the austral spring and summer months (Oliveira et al., 2014). The dry season varies in length depending on the region, being shorter in the south than in the core or elsewhere (Cassino, Ledru, de Almeida Santos, & Favier, 2020; Souza et al., 2015).

The structure and composition of the Cerrado vegetation and its geographical range were strongly affected by wet/dry events during the late Pleistocene and Holocene, with marked differences between south and central areas (Cassino et al., 2020). In the south (Cerrado-Atlantic Forest Transition), the lower temperatures and more frequent winter rains reduce the evaporative demand and the strength of the dry season (Melo & Durigan 2011). Low-intensity frosts are frequent in southern Brazilian savannas, occurring almost annually (Brando & Durigan 2005), but severe frost events can also occur (Hoffmann et al., 2019). By contrast, in the core region, the high atmospheric evaporative demand during the extended dry season (see Appendix A: Fig. 1) imposes a prolonged water stress (Meinzer et al., 1999), which is reflected in several plant strategies to maintain plant water balance that are associated with leaf phenology (Franco et al., 2005), and a higher probability of more intense and recurrent fire regimes (Hoffmann, Schroeder, & Jackson, 2002). In the northern periphery (Cerrado-Amazonia Transition), typical cerrado is marked by 58% higher biomass compared to central areas (Morandi et al., 2020), which may be explained by the higher temperature and precipitation compared to the core region. These differences are reflected in some plant functional traits, such as south periphery species showing higher leaf nutrient concentrations and specific leaf area compared to core species (Souza et al., 2015) and intraspecific leaf trait variability in widespread species across the Cerrado (Buzatti et al., 2019; Ribeiro et al., 2016). Despite their importance, these studies have not focused on traits that enhance plant survival in seasonally dry fire-prone environments.

Bark performs many different functions in plants and plays an important role for plant fitness, but most studies in savannas interpreted bark traits, particularly bark thickness

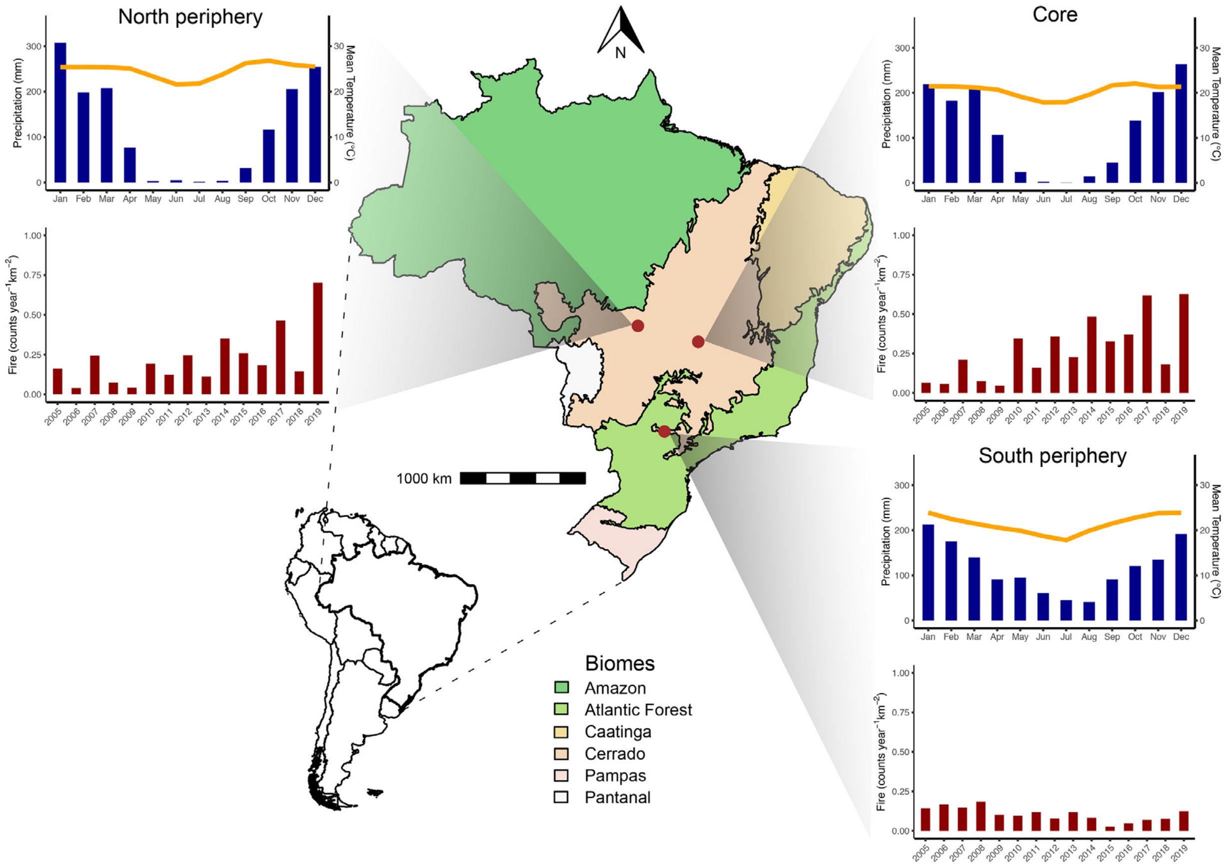

Fig. 1. Sampling sites, climatic conditions and fire regimes. The map of Brazil shows the location of our three sites in the Cerrado (core region in Brasília − DF; north periphery region in Nova Xavantina − MT; and south periphery region in Assis − SP). Brazilian Biomes according to IBGE (2004) classification are depicted in different colours. Top bar plots show the average accumulated precipitation per month (blue bars) and mean monthly temperature (orange line) for a 10-year period (2000−2011) per site. Bottom bar plots show fire counts per year per km^2 from 2005 to 2019 measured by satellite images (red bars). Precipitation and temperature data were obtained from INMET (Instituto Nacional de Meteorolologia −http://www.inmet.gov.br) and fire counts per year were obtained from INPE (Instituto Nacional de Pesquisas Espaciais - http://www.inpe.br/queimadas) and divided by the municipality area to obtain the average of fire counts per km^2 (see Appendix A: Table 1 for details).

variation, being the result of selective pressures imposed by fire regimes (Pellegrini et al., 2017; Rosell, 2019). Other bark functions are less studied despite the key role played by this structure in plant water relations, thermal insulation and carbon balance (Loram-Lourenço et al., 2020; Rosell, 2019). Studies integrating the multiple functions of the bark and different selective pressures or on sets of co-varying bark traits are scarce. Moreover, these patterns of variation across distinct communities within a broad geographical range in seasonally dry fire-prone savannas have not yet been investigated.

In woody species, bark refers to all tissues in the main stem, branches and twigs outside the vascular cambium, including the secondary phloem, periderm and rhytidome (Evert, 2006). Bark morphological variation is noticeable at the plant community level, suggesting a coordination between the different physiological and ecological functions in order to increase species survival and fitness according to the local environmental conditions (Rosell, Gleason, Méndez-Alonzo, Chang, & Westoby, 2014), and even at the ontogenetic level, e.g. the relationship between tree diameter and main stem relative bark thickness changes as trees grow (Schafer, Breslow, Hohmann, & Hoffmann, 2015). Because of its structural complexity, bark is involved in different processes, such as water and soluble carbohydrate storage (Scholz et al., 2007), and protection against fire in fire-prone environments (Hoffmann & Solbrig 2003; Pausas, 2015). Bark is often divided into the inner living portion, which includes the innermost area of the periderm, and the non-living outer portion, composed of dead cells. The wide variation in inner and outer bark thickness across species reflects trade-offs between different bark functions (Rosell et al., 2014). For example, inner bark is associated with water and carbohydrate storage, while the outer bark insulates the living tissues against extreme temperatures. Indeed, these two functions might be equally important for tree recovery and survival in seasonally dry and fire-prone environments such as the Cerrado (Scalon et al., 2020).

Here, we investigated differences in bark morphological traits and in the allometric relationships of branches and main stem bark traits in three typical cerrado communities, differing in fire history and climate, one located at the core region of the Cerrado in Central Brazil and the other two at its periphery in the transition zones with the Amazon and the Atlantic Forest. We hypothesized that woody species from the periphery areas of the biome will show divergent bark traits from core species, because of differences in the strength exerted by abiotic filters (i.e., rainfall seasonality and fire frequency). We expected that (I) the core plant community will show higher inner and outer bark thickness, resulting in higher total bark thickness, since species are under higher water deficit and higher risk of fire compared to species occurring in the periphery (Fig. 1, Appendix A: Fig. 1); (II) south periphery plant community will show thinner bark with higher moisture content (BMC), and consequently lower bark density (Poorter, McNeil, Hurtado, Prins, & Putz, 2014), because they have more access to water throughout the year and fires are less frequent; and (III) south periphery species will also show tighter stem-twig bark trait associations compared to core and north periphery species, since species from the latter regions would possibly allocate proportionally more carbon (i.e., deploying a thicker bark) to the main stem outer bark to better insulate the living tissues and thus reducing the chance of topkill by fires (Rosell, Castorena, Laws, & Westoby, 2015). Specifically, because surface fires predominate in the Cerrado savannas, we expected species from the core and north periphery regions to have greater investment in bark of the main stem, which would confer greater stem survival, while species from the south periphery may equally distribute the bark investment between main stem and branches.

Materials and methods

We sampled sites in the core and in the southern and northern periphery of the Cerrado biome on different field campaigns during 2015 and 2016 (Fig. 1). The average annual precipitation in the core area is approximately 1453 mm, while the south periphery precipitation averages 1300 mm and the north periphery, 1550 mm (INMET, Instituto Nacional de Meteorolologia −http://www.inmet.gov.br). In the core, the dry season occurs from May through September and the mean monthly temperature is 22.5 °C, ranging from 19 to 23 °C (Oliveira, Dawson, & Burgess, 2005). In the south periphery the dry season is shorter and less pronounced, from June to August, and the mean monthly temperature ranges from 16.9 to 24.3 °C (Melo & Durigan 2011; Souza et al., 2015), while in the north periphery the dry season is longer, from April to September, and mean monthly temperature is 25 °C, ranging from 21.5 to 28 °C (Marimon, Felfili, Lima, Duarte, & Marimon-Júnior, 2010). Sites are characterized by a pronounced dry season and climate type Aw (core and north periphery) and Cfa (south periphery), according to Köppen's classification. All sites occur in highly acidic, deep and well-drained soils with low-nutrient availability (Reatto, Correia, & Spera, 1998). There are marked differences in fire frequency between regions (Fig. 1). Comparing between the three regions for the whole time series of 14 years (see Appendix A: Table 1 for calculation details), the core region averaged ~0.28 ± 0.19 (mean ± sd) fire counts per year per km^2, similar to the north periphery region (~0.22 ± 0.17). Fire frequency was ~2-fold lower in the south periphery region (~0.10 ± 0.04). Human activities cannot be fully excluded, since the increasing Cerrado occupancy has altered natural fire regime and increased fire frequency (da Silva Junior et al., 2020).

The study sites located in the southern periphery of the Cerrado (south periphery) were both located in protected areas of São Paulo State (Brazil), the Floresta Estadual de Assis (-22.62, -50.36) and the Estação Ecológica de Santa Bárbara (-22.82, -49.23). The two areas are approximately 130 km from each other, but are similar in floristic composition, climate and edaphic characteristics (Durigan, Garrido, Max, & Tabanez, 1995; Melo & Durigan 2011). They are both located in a transition zone between Cerrado and tropical Atlantic Forest biome. The northern periphery site (north periphery) was in the Bacaba Municipal Park at Nova Xavantina, Mato Grosso, Brazil (-14.43, -52.21), in the transition between Amazon Forest and Cerrado biomes. The site in the core of the biome (hereafter, core) was located at the 'Roncador' Ecological Reserve from the Brazilian Institute of Geography and Statistics (RECOR / IBGE), 33 km south of Brasília, Federal District, Brazil (-15.56, -47.53).

In all regions, we strictly sampled typical cerrado vegetation during the rainy season (south periphery in November 2015, core in January 2016 and north periphery in December 2017). According to Ribeiro and Walter (1998), the typical cerrado is a cerrado *sensu stricto* subtype with 20 to 50% of tree cover and tree heights between 3 and 6 m. We chose the most abundant woody tree species at each region based on basal area contribution (>80% basal area contribution for individuals with more than 5 cm diameter at 30 cm aboveground according to previous inventories in 1 ha plots) in order to characterize the respective plant community (see Appendix A: Table 2). We sampled 20 species from the core, 20 species from the south periphery and 24 species from the north periphery region, totalling 51 tree species representing 19 different families (see Appendix A: Table 2). All sampled species occur typically in savanna vegetation (Ratter, Bridgewater, & Ribeiro, 2003). Two species were sampled in all sites (*Qualea grandiflora* and *Roupala montana*). They are commonly found and of widespread occurrence in the biome (Ratter et al., 2003). For each species, we randomly selected five individuals, removed a 2 × 2 cm sample of bark from the main stem at 30 cm above the ground and collected a secondary branch of approximately 1 cm diameter and 5 cm length from each sampled individual. In the field, we measured inner and outer bark thickness from the main stem and the branch using a digital calliper (0.001 mm). Inner and outer bark were generally easily distinguished visually, but we used a magnifying lens to confirm our classification whenever there was any uncertainty. We also measured the sampled branch diameter and tree diameter at the same height the samples were removed. Bark samples of the stems were placed in hermetically closed recipients and taken to the laboratory for measurements of bark volume by the water displacement method and fresh mass with a scale (0.001 g). After oven drying samples for 72 h at 75 °C, we measured bark dry mass and calculated bark density (BD, the ratio of dry bark mass to fresh bark volume) and bark moisture content (BMC, the difference between fresh and dried bark mass divided by bark fresh volume).

Because tree diameter differed between regions (see Appendix A: Table 2), and the relationship between tree diameter and main stem relative bark thickness does not remain constant as trees grow and varies amongst species (Schafer et al., 2015), the use of relative bark trait values could potentially bias our results. To circumvent this problem, we performed linear mixed models with random intercepts for each $\log_{10}$-transformed bark trait separately. We then predicted bark traits at standardized stem size of 10 cm diameter for each species (median of tree diameter across all individuals was 9.6 cm). By controlling for a fixed stem size it is possible to correctly compare intrinsic differences in bark traits, disregarding a possible sampling bias in tree diameter. Bark traits of branches were used without transformation, since the branch size was standardized for all species in all sites (~1 cm). Relative bark thickness (inner, outer, total) for branches and for the standardized 10 cm diameter stem was calculated as the ratio of bark thickness to branch or stem radius × 100 % (Hoffmann et al., 2012).

Statistical analysis

All analyses were performed using software R version 3.6.1. We calculated an aridity index using the function ‘arid’ from the package ‘ClimClass’ (Eccel, Cordano, Toller, Zottele, & Eccel, 2015) to compare annual and monthly water deficit experienced by the vegetation between the three regions, according to De Martonne (1926). Data normality and homogeneity of variance was checked using Shapiro−Wilk and Levene tests respectively, and variables were $\log_{10}$-transformed for normality assumptions when necessary. However, all data was $\log_{10}$-transformed before bivariate line-fitting using standardised major axis (SMA), which is more appropriate for allometric relations (Warton, Wright, Falster, & Westoby, 2006).

To test our first and second hypotheses and account for general differences between bark traits from the different Cerrado regions, we used one-way analyses of variance (ANOVA) followed by Tukey tests, with species as our statistical unit. For the two common species found in all three sites, we performed individual ANOVAs to investigate if trends at the community level were maintained within the same species across the three regions. We also tested for differences between the three plant communities in bivariate relationships of bark traits using the package SMATR (Warton, Duursma, Falster, & Taskinen, 2012). To verify if the bark trait composition amongst the individuals and regions were similar, we used a Principal Coordinates Analysis (PCoA, Gower (1966)) using Euclidean distances of the standardized trait per individual matrix. PCoA was chosen because it allows us to graphically visualize a square matrix that describes the similarity or dissimilarity between individuals. To evaluate if the trait space of the regions were similar, we drew a convex hull linking the points of the individuals sampled in the same region.

Bivariate relationships were used to test our third hypothesis, that south periphery species will show tighter stem-twig bark trait associations compared to core and north periphery species. The strength of bivariate relationship were quantified using the coefficient of determination (r^2). To test for differences in standardized major-axis (SMA) slopes and intercepts, we applied the Wald test (Warton et al., 2006). For all tests, differences were considered significant at $P \leq 0.05$.

Results

Sites differed in aridity, with core (Ia = 44.98) and north periphery (Ia = 45.32) regions similarly drier than the south periphery (Ia = 55.55), especially during the dry season (i.e., May to September, see Appendix A: Fig. 1). Species from the core and north periphery regions showed lower diameter and had a thicker total bark compared to south periphery species (see Appendix A: Table 3). Overall, there was no difference between core and periphery species for bark density and bark water content (Table 1, see Appendix A: Table 3). We found no differences between the three regions for relative outer bark thickness; however, core and north periphery species had thicker inner bark than south periphery species, reflected in thicker relative total bark (Table 1, see Appendix A: Fig. 2). These differences in main stem bark thickness were maintained for standardized 10 cm diameter values (Table 1), untransformed relative values (see Appendix A: Table 3), and for the two species that occurred in the three regions (see Appendix A: Fig. 3). For standardized 10 cm stems, bark of core and north periphery species accounted for ~30 % of the stem diameter but only ~ 20 % for south periphery species.

Branches from species in the core had thicker total and inner bark than periphery species (Table 1). The PCoA scatterplot showed that the bark trait composition of the species in the core region is a nested sample from the trait composition in the northern and southern regions (Fig. 2). This nested pattern reflected the absence of individuals with thinner branch bark in the core region (Table 1).

Absolute total bark thickness (TBT) and tree diameter scaled positively for core, north and south species (Fig. 3A).

Table 1. Values (mean ± sd), ranges and *P*-values of the one-way ANOVAs for bark traits at standardized stem size of 10 cm diameter measured in the core and in the north and south peripheries of the Cerrado.

Trait	Core (range)	North Periphery (range)	South Periphery (range)	*P*-value
TBT_{10}	30.52 ± 7.13^{a}	29.06 ± 7.16^{a}	23.52 ± 8.56^{b}	**0.015**
(%)	(14.98 − 42.86)	(17.93 − 42.19)	(6.21 − 38.00)	
IBT_{10}	13.58 ± 5.11^{a}	12.10 ± 4.35^{a}	8.72 ± 2.73^{b}	**0.002**
(%)	(5.63 − 27.44)	(6.45 − 21.01)	(2.47 − 15.57)	
OBT_{10}	15.56 ± 9.16	16.40 ± 10.73	12.98 ± 7.81	0.483
(%)	(1.73− 34.55)	(0.71 − 33.92)	(2.05 − 24.79)	
BWC_{10}	34.93 ± 15.41	31.71 ± 15.43	36.66 ± 15.08	0.464
(%)	(10.99 − 66.82)	(14.15 − 62.32)	(14.80 − 65.08)	
BD_{10}	0.38 ± 0.09	0.39 ± 0.10	0.32 ± 0.07	0.058
(g cm^{-3})	(0.23 − 0.58)	(0.22 − 0.58)	(0.22 − 0.47)	
TBT_{branch}	51.38 ± 11.81^{a}	37.05 ± 12.73^{b}	31.37 ± 10.79^{b}	< **0.001**
(%)	(27.16 − 78.40)	(19.48 − 77.77)	(14.12 − 50.47)	
IBT_{branch}	34.90 ± 9.87^{a}	24.34 ± 10.08^{b}	21.69 ± 8.06^{b}	<**0.001**
(%)	(18.61 − 48.16)	(6.29 − 45.52)	(6.74 − 32.61)	
OBT_{branch}	17.51 ± 10.81	12.71 ± 13.85	9.29 ± 11.75	0.152
(%)	(1.06 − 42.72)	(0.73 − 58.23)	(0.85 − 41.12)	

Bark samples were removed from the main stem at 30 cm above the ground and from a secondary branch of approximately 1 cm diameter and 5 cm length from each sampled individual. Main stem total bark thickness (TBT_{10}), main stem inner bark thickness (IBT_{10}), main stem outer bark thickness (OBT_{10}), main stem bark water content (BWC_{10}), main stem bark density (BD_{10}), branch total bark thickness (TBT_{branch}), branch inner bark thickness (IBT_{branch}), and branch outer bark thickness (OBT_{branch}). Bark thickness (inner, outer and total) expressed as a percentage of branch or the standardized stem radius. Different letters indicate significant differences according to Tukey's test ($P \leq 0.05$). Bold means significant effect ($P \leq 0.05$).

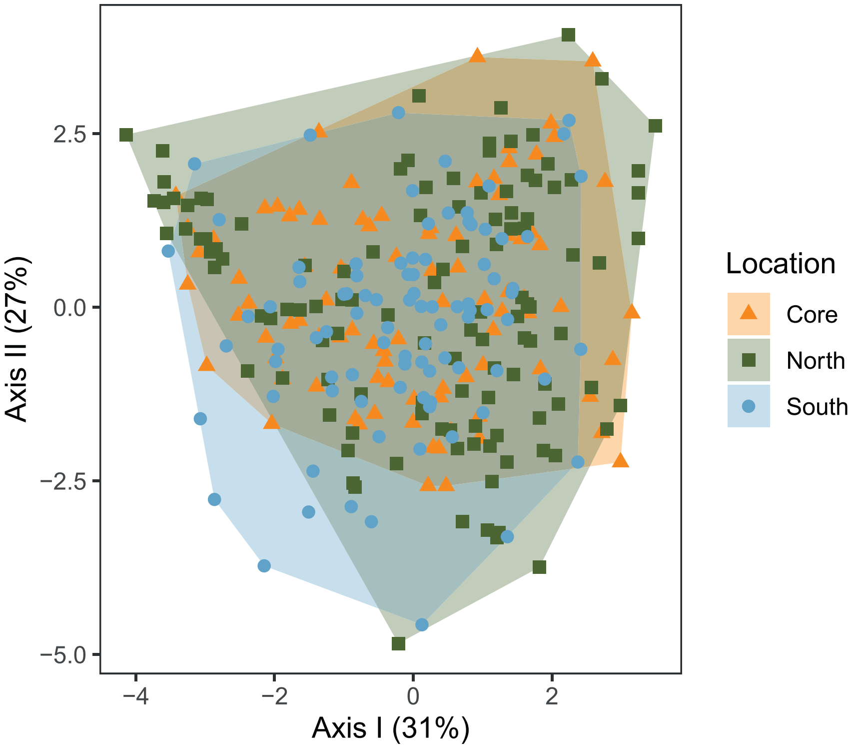

Fig. 2. Scatter diagram of the first two PCoA axes of bark traits of the Cerrado species from Central Brazil (core, orange triangles), northern limits of the biome (green squares) and southern limits of the biome (blue circles). The polygons linking the points are depicting the trait space of the core (orange), north periphery (green) and south periphery (blue). Each data point represents a single individual.

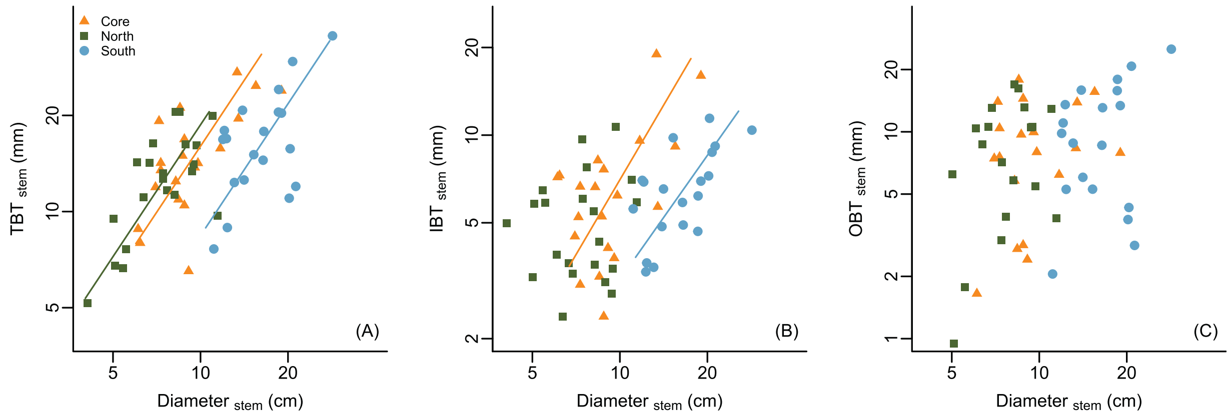

Fig. 3. Relationship between stem diameter and (A) total bark thickness; (B) inner bark thickness; and (C) outer bark thickness for Cerrado species from Central Brazil (core, orange triangles), north limits of the biome (north periphery, green squares), and south limits of the biome (south periphery, blue circles). Each data point represents different species (averaged from 5 individuals). Significant regression slopes ($P < 0.05$) shown as solid lines. Correlation r and P-values are shown in Appendix A: Table 4.

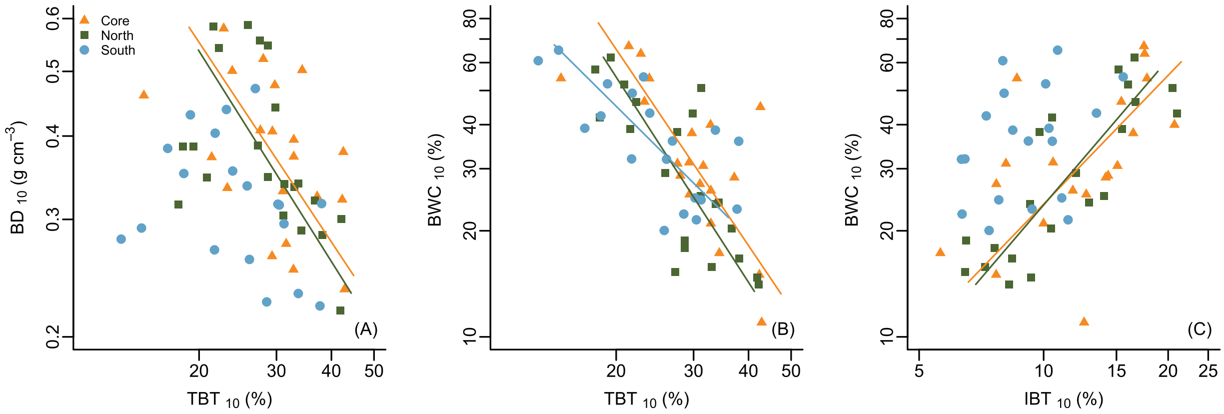

Fig. 4. Relationship between bark traits at standardized stem size of 10 cm diameter for Cerrado species from Central Brazil (core, orange triangles), north limits of the biome (north periphery, green squares) and south limits of the biome (south periphery, blue circles): (A) total bark thickness (TBT_{10}) and bark density (BD_{10}); (B) total bark thickness (TBT_{10}) and bark water content (BWC_{10}); (C) inner bark thickness (IBT_{10}) and bark water content (BWC_{10}). Inner and total bark thickness expressed as a percentage of the standardized stem radius of 5 cm. Each data point represents different species. Significant regression slopes ($P < 0.05$) shown as solid lines. Correlation r and P-values are shown in Appendix A: Table 4.

Although SMA slopes were not significantly different (Wald statistic: 0.0002, $P = 0.987$) at any given diameter, core and north species tended to show 50% higher total bark thickness compared to south species (difference in the intercept: Wald statistic: 17.72, $P < 0.001$, Fig. 3A). Absolute inner bark thickness also scaled with stem diameter except for north species, however, slopes between core and south species were significantly different (Wald statistic: 7.24, $P = 0.007$, Fig. 3B). Across species, outer bark was not related to stem diameter for any Cerrado region (Fig. 3C). There was no correlation between inner and outer bark for either main stem ($r^2 = 0.01$, $P = 0.552$) or branches ($r^2 = 0.02$, $P = 0.367$) for the three regions together, or for each region individually, suggesting distinct functional roles for each bark section.

Bark thickness was negatively related to bark density for core and north species, meaning that thinner bark tended to be denser within these communities, but this was not evident for south species (Fig. 4A). Bark water content was negatively related to total bark thickness (Fig. 4B) for all regions, but positively related to inner bark thickness for core and north species (Fig. 4C).

Stem and branch total bark thickness were related only for periphery species (Fig. 5A). Outer bark thickness was highly correlated between branches and stems for all regions (Fig. 5B), with no differences in slopes and intercepts (Wald statistic: all $P > 0.05$), while main stem inner bark was not related to branch inner bark thickness for any of the Cerrado regions (Fig. 5C).

Discussion

We compared branches and main stem bark traits of three tree communities with different shifts in tree species dominance across the Cerrado range to investigate whether

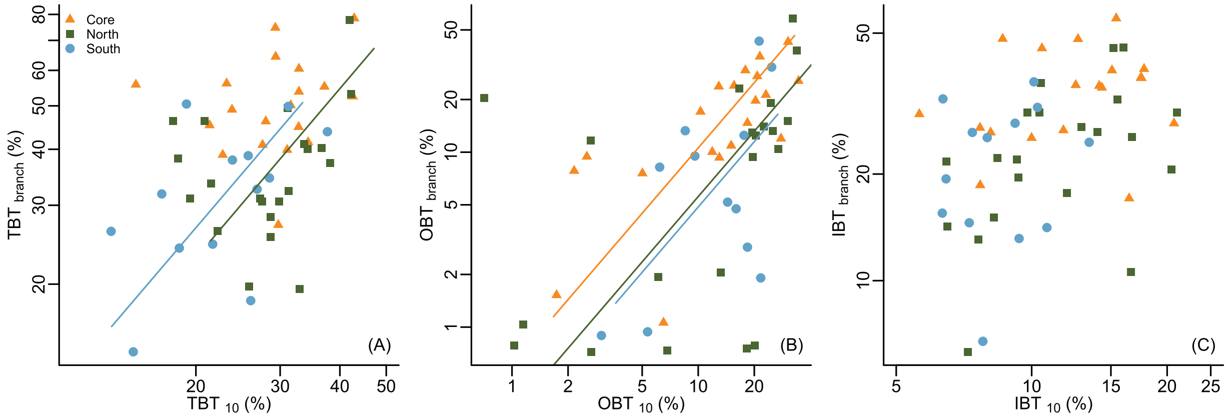

Fig. 5. Relationship between bark traits at standardized stem size of 10 cm diameter and bark traits for 1 cm diameter branches for Cerrado species from Central Brazil (core, orange triangles), north limits of the biome (north periphery, green squares) and south limits of the biome (south periphery, blue circles): (A) total (TBT), (B) outer (OBT) and (C) inner bark thickness (IBT). Inner, outer and total bark thickness expressed as a percentage of the branch or stem radius. Each data point represents a different species. Significant regression slopes ($P < 0.05$) shown as solid lines. Correlation r and *P*-values are shown in Appendix A: Table 4.

distinct environmental drivers could influence bark structure and allocation across species. We found that outer bark thickness showed low variability across tree communities, with no difference in the investment in branches and main stem outer bark between core and periphery dominant species (Table 1). Moreover, there was a common relationship between branches and main stem outer bark thickness, suggesting a conservative strategy in the activity of the tissue that forms the outer bark (i.e., phellogen), with proportional allocation across the individual trees, irrespective of fire activity and site characteristics. This lack of difference in phellogen activity was recently shown in different studies with Cerrado woody species occurring in savanna and adjacent forest areas (Blagitz, Machado, & Marcati, 2019; Maracahipes et al., 2018), indicating that, within and between species, outer bark thickness did not vary with different environmental conditions. Our results add to these findings by showing that outer bark thickness also does not seem to vary widely across the three distinct plant communities within the same vegetation type, despite different fire counts per year in the short-term (Fig. 1) and likely differences in fire histories (Cassino et al., 2020). There is a general relationship that the degree of heat insulation increases with the square of bark thickness (Pausas, 2015). However, bark properties are also involve in protection against low temperatures (De Antonio, Scalon, & Rossatto, 2020) and frosts are a recurrent event in the south Cerrado range (Brando & Durigan 2005). In fact, frost and fire events cause similar damage to internal stem, branches and leaf tissues, affecting plant growth and persistence in the environment (Hoffmann et al., 2019), and the thermal insulation provided by the outer bark may be an important trait throughout the Cerrado range.

We have also shown that the living portion of the bark (i.e., the inner bark) was the main driver of the observed differences in relative total bark thickness, where species from the core and north periphery region showed thicker total and inner main stem bark. For branches, inner bark thickness was consistently higher in the core species, but similar between south and north periphery. Taken together, these differences were reflected in a larger trait space occupied by species occurring in the periphery of the biome, while core species were more restricted (Fig. 2), which suggests stronger environmental filters constraining functional diversity of bark traits in the central areas of Cerrado. This environmental filtering hypothesis might be further tested under experimental conditions, such as considering post-fire responses (Scalon et al., 2020). The same general pattern was observed for the two species that occurred in the three distinct regions (see Appendix A: Fig. 3), especially for *Q. grandiflora*, suggesting that the environment, more than community composition drives these observed differences.

Our results generally agree with those of Rosell (2016), who found a weak relationship between outer bark and stem diameter considering over 600 plant species spanning 18 sites worldwide, suggesting that outer bark does not have a particular metabolic role as inner bark does. For all regions, main stem outer bark did not scale with stem diameter, while total and inner bark thickness did (except for north periphery species; Fig. 3). In addition, the lack of correlation between inner and outer bark for both stem and branches emphasize the different bark functions exerted by each bark portion independently. Inner bark consists of living cells with a high proportion of parenchyma, and is thought to have a fundamental role in water storage and the photosynthate-translocating secondary phloem (Scholz et al., 2007). In fact, Rosell (2016) found that inner bark tended to be thicker in drier and warmer environments, proposing a storage role to buffer against fluctuation in water potential and protect the transpiration stream in highly unstable water availability environments under high evapotranspiration rates. Recently, Loram-Lourenço et al. (2020) showed that water storage and transport was related to inner bark thickness for 31 Cerrado woody species. Indeed, relative inner bark thickness was strongly and positively correlated with bark water content, but only for the core and north periphery (Fig. 4C), the regions with thicker inner bark (Table 1), which suggests that the trees allocate more resources to build thicker inner bark in order to transport assimilates or store water in comparison to south periphery species. This difference may be related to the higher water deficit in the north and core regions, with longer dry season (5−6 months length), higher mean temperatures and higher aridity (Fig. 1, see Appendix A: Fig. 1). Branches and main stem outer bark and bark density, which are possibly more related to fire protection (Loram-Lourenço et al., 2020) and internal tissue insulation against extreme temperatures (De Antonio et al., 2020), surprisingly did not differ between the three regions. Therefore, we suggest that differences in bark traits between the three Cerrado regions might not only be related to fire and frost occurrence, but also to differences in water availability and seasonality of rainfall.

Nevertheless, bark moisture content is also related to increased fire resistance and can be important in explaining tree susceptibility to top-kill (Higgins et al., 2012). Indeed, for Cerrado species, inner bark may provide more insulation than outer bark (Scholz et al., 2007) and, in addition, serve as a significant source of water during the driest period of the day (Bucci et al., 2005). Therefore, investing in thicker inner bark is a clear advantage in seasonally dry and fire-prone environments, such as the Cerrado. Recently, Scalon et al. (2020) have shown that there are three distinct main ecological strategies that Cerrado trees might adopt to survive and recover after fire, either by investing in thicker inner bark and high bark water content, or in fast growth rate, plant height and high bark density, or in a thicker outer bark and high wood density with high bud protection. Here, we did not investigate these different strategies but, based on our results, we can speculate that investing in inner bark thickness and bark moisture may be a more recurrent and common strategy, at least in plant communities exposed to high evaporative demand during a long period and prone to a high risk of fire.

Considering investment in branch bark, similarities were stronger between the two periphery sites. While we expected that plant communities differing in fire history would differ in the carbon investment in bark across the different portions of their trunk (Rosell et al., 2015), differences were, again, only in inner bark investment. While north periphery species maintain a proportional investment between branch and stem inner bark, core species tend to invest proportionally more in inner bark in the main stem, and south periphery species shift the inner bark investment to the branches. There is a probable trade-off between investing in a thick bark to protect the branches against fire, or in a thinner bark containing chlorophyll, where light penetration and CO_2 permeability could promote high rates of recycling photosynthesis, and support hydraulic function in the sapwood (Cernusak & Cheesman 2015; Rosell et al., 2014). Bark recycling photosynthesis should be advantageous in hot and dry environments, because it increases the whole plant water-use efficiency offsetting carbon costs (Vandegehuchte, Bloemen, Vergeynst, & Steppe, 2015). Since we noticed a high proportion of branches with inner bark presenting green colour (personal observation), which indicates the presence of chlorophyll, we suggest that differences in inner bark investment between Cerrado communities may perhaps reflect differences in bark recycling photosynthesis. Despite being described for many species from water-stressed environments, this mechanism has not been reported for Cerrado species, and future research is needed to quantify the amount of carbon assimilation that could be involved in this process.

Other factors can affect the observed differences in inner bark investment and scaling relationships, such as fire behaviour, inner bark anatomical properties, and rooting patterns influencing soil water access. Most savanna fires are surface fires fuelled by the herbaceous layer with brief periods of high temperatures (Miranda, Sato, Neto, & Aires, 2009), however, differences in relative humidity and aridity index between the three regions might also reflect differences in fire severity, since the climate may influence fuel moisture content and, in turn, fire intensity and flame height (Rissi, Baeza, Gorgone-Barbosa, Zupo, & Fidelis, 2017). Inner bark, which includes secondary phloem, cortex and phelloderm (Rosell, Olson, Anfodillo, & Martínez-Méndez, 2017), is rich in parenchymatic cells and varies between species and through ontogeny in relation to the proportional amount of living tissue and cell wall thickness (Rosell et al., 2015). The sapwood and the inner bark are the main water storage compartments that, despite generally exhibiting different biophysical properties (Scholz et al., 2007), are not likely to operate in isolation (Niklas, 1999). Cerrado trees have different root typologies that are associated with leaf phenology patterns (Jackson et al., 1999; Scholz et al., 2008). Rooting patterns define access to different soil water sources and affect the potential of overnight recharge of water storage compartments. These characteristics will constrain the tree's potential size and affect the amount of water that is seasonally available to regulate diurnal water deficits, further influencing the need of exerting stomatal control of transpiration driven by the evaporative demand of the atmosphere. Further work is needed to better investigate the root-associated mechanisms and selective pressures underlying the observed patterns and trade-offs of functional diversity in bark traits of Cerrado trees.

In conclusion, we have shown that major differences in structural and functional properties of bark components in species across the Cerrado range were related to the investment in inner bark of main stem and branches, while outer bark was very similar. It is widely known that fire acts as an important environmental driver, and co-occurring species in fire-prone environments are expected to share similar morphological and physiological traits, such as corky and thicker outer bark. Here we show that the combination of strong seasonality and fire frequency may favour higher investment in inner bark thickness to support high water storage and, at the same time, to provide cambium heat insulation in the eventual case of a fire event.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2021.06.011.

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