

The lanky and the corky: fire-escape strategies in savanna woody species

Vinícius de L. Dantas¹ and Juli G. Pausas^{2*}

¹Department of Botany, Universidade Federal de São Carlos, PO Box 676, 13565-905 São Carlos, SP, Brazil; and

²CIDE-CSIC, Ctra. Nàquera Km. 4.5 (IVIA), 46113 Montcada, Valencia, Spain

Summary

1. Fire and herbivory are the main disturbances shaping the structure of savannas. In these ecosystems, the key strategies by which woody plants escape fire are either early height growth (the *lanky* strategy) or early bark growth (the *corky* strategy). We hypothesize that the dominance of each strategy in different savannas depends on the prevailing disturbance regimes. Given the importance of herbivory in afrotropical savanna, we expect woody plants in these savannas to be taller and have thinner barks (the *lanky* strategy) than plants in neotropical savanna where fire tends to be more intense (the *corky* strategy).

2. We compiled data on bark thickness and stem height in relation to stem diameter for afrotropical and neotropical savanna woody species and tested for differences in the allometric relationship between these two savannas with a general linear mixed model (GLMM).

3. Fire intensities were higher in neotropical than in afrotropical savannas. Afrotropical savanna plants were taller and had thinner barks for a given diameter than neotropical savanna plants – supporting our hypothesis that because of the contrasting disturbance regimes, the *lanky* strategy is more adaptive in afrotropical savannas, whereas the *corky* strategy is more adaptive in neotropical savannas.

4. Synthesis. While the *lanky* strategy is more associated with heavily browsed and fuel-controlled savannas, the *corky* strategy is associated with lightly browsed savannas that experience more intense fires. Because the relative role of disturbances varies across the globe, we suggest that the height-bark-diameter scheme is a powerful framework for understanding the ecology of many savannas.

Key-words: African savannas, bark thickness, cerrado, consumer control, disturbance regime, fire intensity, fire-escape strategies, herbivory, plant development and life-history traits, tree height

Introduction

The savanna is a major terrestrial biome, covering one-sixth of the world's land surface (Grace *et al.* 2006). Fire plays a fundamental role in the maintenance of savannas by regulating the stability of tree-grass coexistence (Higgins, Bond & Trollope 2000; Bond, Woodward & Midgley 2005; Bond 2008; Murphy & Bowman 2012). In these systems, fire affects the woody vegetation by topkilling juvenile trees before they become fire resistant and thus preventing them from growing to larger size classes (Bond & van Wilgen 1996; Gignoux, Clobert & Menaut 1997; Higgins *et al.* 2007; Hoffmann *et al.* 2009). This effect generates a demographic bottleneck that increases the dominance of short and juvenile woody plants (the 'Gulliver' syndrome; Bond & van Wilgen 1996; Higgins *et al.* 2007). The transition from below to above this 'fire trap' is a major constriction on tropical

savannas (Bond, Cook & Williams 2012; Hoffmann *et al.* 2012) and is largely dependent on fire regimes (Gill & Ashton 1968; Gignoux, Clobert & Menaut 1997; Bond 2008; Hoffmann *et al.* 2012; Murphy & Bowman 2012).

Despite the generality of fire control on savannas, herbivory and climate may also have important direct and indirect effects (Bond 2008; Asner *et al.* 2009; Midgley, Lawes & Chamaillé-Jammes 2010; Murphy & Bowman 2012). Herbivory may generate demographic bottlenecks in a similar way to fire (Asner *et al.* 2009; Staver *et al.* 2009; Midgley, Lawes & Chamaillé-Jammes 2010; Moncrieff *et al.* 2011). For instance, browsers and grazers may slow the growth of trees by feeding on juvenile plants (Bond 2008; Scogings, Mamashela & Zobolo 2012) and foraging in recently burned areas (Fuhlendorf *et al.* 2008). In fact, the synergistic effect of fire and browsing plays an important demographic role in the structure of heavily browsed savannas (Staver *et al.* 2009; Moncrieff *et al.* 2011). The effects of grazers on woody plants may also be indirect because they reduce fuel loads by consuming biomass and favouring less-productive

*Correspondence author. E-mail: juli.g.pausas@uv.es

grazing-adapted grasses (Archibald *et al.* 2005; Savadogo *et al.* 2007; Bond, Smythe & Balfour 2008). This fuel reduction results in fires of lower intensity than in lightly grazed savannas (Archibald *et al.* 2005; Savadogo *et al.* 2007). In addition, the rainfall regime strongly controls C₄ grass productivity (Fay *et al.* 2003; Sankaran *et al.* 2005) and is an important factor affecting the flammability of savannas (Higgins, Bond & Trollope 2000). This variability of factors and the wide distribution of the savanna biome results in savannas around the globe being subject to different disturbance regimes and hosting woody florae with distinct fire-escape strategies (Bond & van Wilgen 1996; Archibald & Bond 2003; Hoffmann *et al.* 2009; Lawes *et al.* 2011a; Higgins *et al.* 2012).

There are two main strategies by which woody plants escape from fire in savannas (Gignoux, Clobert & Menaut 1997). In the first strategy, plants escape by quickly growing in height to locate the canopy above the flame zone before the next fire (*hide-and-resprout* according to Gignoux, Clobert & Menaut 1997; Wakeling, Staver & Bond 2011). These plants tend to have a pole-like or lanky architecture (the *lanky* strategy hereafter; see Fig. 9b in Archibald & Bond 2003 for an example) and failure to grow enough during the inter-fire period results in top-killing followed by basal resprouting. Because building a tall canopy is also adaptive against large browsers, it should also be particularly important in heavily browsed savannas (Bond, Cook & Williams 2012). The second strategy includes plants allocating resources to thick heat-insulating barks that enable plants to stay and resist fire (Gignoux, Clobert & Menaut 1997; Fig. 1; the *corky* strategy hereafter). By investing early in insulating barks, these species protect the meristem from heat and are able to resprout



Fig. 1. *Diospyros hispida* A.DC. (Ebenaceae), a South American example of the corky strategy. Although the trunk was fully burned 1 year earlier (dark branches and trunk), the bark protected the lateral buds which enabled epicormic resprouting and the formation of lateral resprouts (light grey branches). This photograph was taken in Emas National Park at the beginning of the rainy season (2011) when this deciduous plant starts to produce new leaves (Photograph: Vinícius de L. Dantas). For an example of the *lanky* strategy, see Archibald & Bond (2003; Fig. 9b).

epicormically after fires (Fig. 1; Medeiros & Miranda 2008; Hoffmann *et al.* 2009; Lawes *et al.* 2011a; Dantas *et al.* 2013; Dantas, Batalha & Pausas in press). Plants presenting the first strategy are predicted to be taller and have thinner barks for a given diameter than plants presenting the second strategy (Gignoux, Clobert & Menaut 1997). Because of the contrasting allocation patterns, *lanky* plants have been hypothesized to be associated with relatively less intense fires than *corky* plants (Vines 1968; Gignoux, Clobert & Menaut 1997). However, while previous studies have demonstrated the importance of each strategy to fire-escape (Hoffmann *et al.* 2009; Higgins *et al.* 2012; Lawes, Midgley & Clarke 2013), none have directly linked their success to the prevailing type of consumer control in savannas.

The savannas of Africa and South America are among the most consumer-controlled ecosystems in the world and are subject to the highest fire frequencies (fire intervals between 1 and 5 years; Bond & Keeley 2005; Bond, Woodward & Midgley 2005; Pausas & Ribeiro 2013). Despite some local variability, fire intensities tend to be lower in afrotropical than in neotropical savannas because the greater herbivore pressure and drier climate in the former limit C₄ grass biomass (Table 1 and Table S1 in the Supporting Information). In these less intense fire regimes, the demographic pressure exerted by herbivores plays a fundamental role in community structure (Staver *et al.* 2009; Moncrieff *et al.* 2011), and the dominance of strategies that avoid both herbivory and fire negative effects is expected. Thus, in these savannas, allocating resources to raise the canopy above the reach of fire and herbivores (the *lanky* strategy) should be more beneficial than building a thick corky bark. In contrast, in neotropical savannas, where the herbivory pressure is lower (Marquis, Diniz & Morais 2001), the *corky* strategy with epicormic resprouting should be fundamental to protecting the stem from more intense fires. Hence, we hypothesized that because of the contrasting disturbance regimes, the *lanky* strategy is more adaptive in afrotropical savannas, while the *corky* strategy is more adaptive in neotropical savannas. This model will be supported if, for a given diameter, African savanna plants have thinner barks and are taller than plants of South American savannas. To evaluate our hypothesis, we began by testing the differences in fire activity and rainfall between neotropical and afrotropical savannas using remote-sensing fire data and global climate information. Then we compiled data on bark thickness, height and diameter for a wide range of woody species growing in several neotropical and afrotropical savannas.

Materials and methods

FIRE AND RAINFALL

To evaluate the fire intensity dissimilarity between afrotropical and neotropical savannas, we compiled fire information obtained from the MODIS sensor on the Terra satellite for the period between January 2001 and December 2009 (the Climate Modeling Grid; Fire Information for Resource Management System, NASA). Specifically,

Table 1. The main factors distinguishing afro-tropical and neo-tropical savannas

	Afrotropical	Neotropical
Mean annual rainfall (mm)	447–1200	1200–2000
Herbivory intensity	High	Low
Mean grass biomass (kg ha ⁻¹)	639–6610	1700–11600
Mean fuel load (kg ha ⁻¹)	2000–9930	5500–12900
Mean fireline intensity (kW m ⁻¹)	25–10906	151–16394
Predicted fire-escape strategy	Lanky	Corky

Full reference sources for this information are presented in Table S1.

we compiled the monthly mean fire radiative power (in megawatts at 0.5° spatial resolution) as a measure of fire intensity (Wooster, Zhukov & Oertel 2003) for the savanna biome in Africa and South America – following the ecoregion approach proposed by Pausas & Ribeiro (2013). For each region, the mean fire radiative power of each pixel was averaged across the whole period (2001–2009). We also assessed the differential rainfall between afro-tropical and neo-tropical savannas by compiling average annual precipitation for the same two regions from WorldClim data (0.0083° spatial resolution; Hijmans *et al.* 2005). We finally compared the mean and frequency distributions of the fire radiative power and annual precipitation for the two savanna regions and computed bootstrap confidence intervals for each region.

TREE DATA COMPILATION

We compiled data relating stem diameter with bark thickness and stem height from 21 published articles – 7 studies on neo-tropical savannas and 14 studies on afro-tropical savannas (see Tables S2 and S3 for details). To extract data published as figures in the articles, we used Web Plot Digitizer (Rohatgi 2012). We complemented the data set with a field sampling in Emas National Park (ENP), central Brazil (see sampling below). Overall, we considered 153 woody species (81 from afro-tropical and 72 from neo-tropical savannas), included in 37 taxonomic families (16 and 28, respectively; see Table S4). Most of the data were at individual level, but we also included some average values. The total sample size was 2294 and 1097 for African savannas (height-to-diameter and bark thickness-to-diameter, respectively) and 1633 and 731 for neo-tropical savannas (height-to-diameter and bark thickness-to-diameter, respectively).

FIELD SAMPLING

We collected data at ENP (central Brazil: 17°49′–18°28′S, 52°39′–53°10′W), a neo-tropical savanna reserve located in central Brazil (Dantas, Batalha & Pausas in press). The reserve has a tropical warm wet climate, with dry winters (Aw type following Köppen 1931). Although the park includes a wide range of physiognomies – from open grassland to closed forest (Dantas, Batalha & Pausas in press) – we only considered data from savannas and open woodlands (the same criteria used in the compilation). We performed the field sampling in the rainy season of 2009/10 on 99 5 × 5 m plots, distributed among different fire ages, representing the current fire history mosaic in the park. We identified all individuals with basal diameter ≥ 3 cm to species and measured bark thickness, basal diameter and stem height for each individual. Bark thickness was measured by inserting a knife in the stem at five haphazardly selected points and measuring the depth of penetration with a digital calliper. Most measurements

were taken on the trunk at 0.3–0.5 m from the ground and then averaged. In some plants, the main stem was very short, bifurcating below 0.3 m; and in these cases, bark thickness was measured halfway from the base to the first bifurcation of the main stem. This sampling approach enabled the inclusion of both rare and common species but still emphasizes the predominant pattern (dominant species) as in the compiled data set. See Dantas, Batalha & Pausas (in press) for further details.

STATISTICAL ANALYSIS

At first we compared the frequency distribution of bark thickness, height and diameter values in the two ecozones including all the compiled data (afro-tropical vs. neo-tropical) using a Wilcoxon rank test. Because the size of the plants differed between ecozones, the subsequent statistical tests were performed considering only the range of overlapping diameters and excluding outliers (as defined by the Tukey's test, that is, excluding values >1.5 times the interquartile range). Because bark thickness and plant height are strongly related to diameter (allometrically), we fitted a general linear mixed model (GLMM) for each escape trait in relation to diameter and with 'species' as random effect. Diameter, height and bark thickness were log-transformed before the analysis. We then included ecozone (afro-tropical vs. neo-tropical) as a fixed factor and tested for significant differences between the two models with a likelihood ratio (LR) test. As different studies in our data set measured diameters at different heights along the stem, we also repeated the analyses using only studies that measured basal diameters – and given that results did not change, these analyses are not reported. All statistical analyses were performed using the 'nlme' and 'stats' libraries from the R software (R Development Core Team 2012).

Results

The remotely sensed fire data (radiative fire power) showed that more intense fires tend to be more frequent in neo-tropical than in afro-tropical savannas (Fig. 2a). Similarly, precipitation tended to be higher in neo-tropical (mean = 1318 mm, CI = 1112.6–1504.9) than in afro-tropical savannas (mean = 832 mm, CI = 697.0–978.63; Fig. 2b). For any of these two variables, the confidence intervals between the two regions overlap (Fig. 2). These results support the tendency observed with the sparse data set compiled from the literature (Table 1).

The analysis of the overall compiled data showed that afro-tropical savanna plants were larger in diameter and height than neo-tropical savanna plants ($P < 0.001$), but they both had similar bark thickness values ($P = 0.61$; Fig. 3). The allometric relationship between bark thickness and diameter significantly differed between ecozones considering either plants of similar sizes (Table 2a) or the entire data set (Table S5a). Similarly, the relationship between stem height and diameter differed significantly between the two ecozones with a significant interaction effect (Table 2b and Table S5b). Inspection of the predicted values indicated that the differences between ecozones are larger for smaller woody plants, but the regression lines do not cross each other. In fact, repeating the analysis for trees of <5 cm in diameter yields a significant difference between ecozones with no significant interaction (Table 2c).

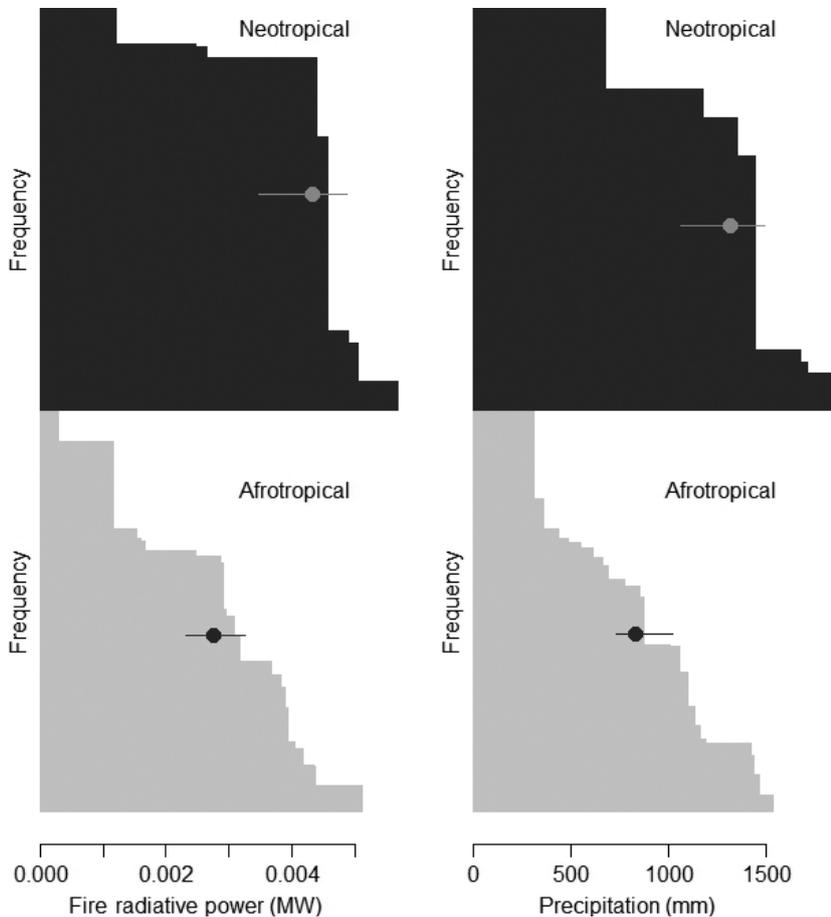


Fig. 2. Frequency distribution of monthly radiative fire power (Megawatt, left) and annual precipitation (mm, right) in afro-tropical (grey bars) and neo-tropical (black bars) savannas. The circles represent the mean value for each region with their upper and lower 95% confidence interval; confidence intervals do not overlap between regions for any of the two variables.

Discussion

As predicted, for a given diameter, afro-tropical savanna plants are taller, whereas neo-tropical savanna plants have thicker barks. These patterns are consistent with our hypothesis that most afro-tropical savanna plants fit the *lanky* strategy of quickly placing the canopy above the flame zone or, otherwise, resprouting from basal buds. In contrast, most of the neo-tropical savanna woody plants fit the *corky* strategy and their stems resist fire thanks to a thick fire-protective bark. Because large mammal herbivory and fire are important factors in many parts of the afro-tropical savanna (Fuhlendorf *et al.* 2008; Staver *et al.* 2009; Moncrieff *et al.* 2011), pole-like trunk architectures (*sensu* Archibald & Bond 2003) with early height growth are more advantageous than either a cage-like architecture (common in heavily browsed low fire frequency savannas; Archibald & Bond 2003) or the corky strategy (typical of savannas with recurrent high-intensity fires; Dantas, Batalha & Pausas in press). Moreover, because fire and herbivory selective pressure are concentrated on the sapling stage (2–3-m-tall plants; Bond 2008; Wakeling, Staver & Bond 2011), differences in height–diameter allometries are especially evident in smaller plants (Table 2). In contrast, the higher annual rainfall (Table 1, Fig. 2) and lower abundance of large mammals in South American savannas (Marquis, Diniz & Morais 2001; Costa *et al.* 2008; Lehmann *et al.* 2011) enable C_4 grasses and shrubs to quickly accumulate. In

these savannas, the typical fuel gap between grasses and mature trees that is observed in most African savannas is often lacking (Dantas *et al.* 2013; Dantas, Batalha & Pausas in press). This results in relatively more intense fires (Table 1 and Fig. 2) that affect thin-barked plants (Hoffmann *et al.* 2009). In such conditions, a thick corky bark is a valuable trait for stem protection and subsequent epicormic resprouting. There is regional to local variation in fire intensity and rainfall (Fig. 2), as well as herbivory, in both afro-tropical and neo-tropical savannas. This is a likely reason that plants with corky and lanky strategies coexist locally (Gignoux, Clobert & Menaut 1997; Rossatto, Hoffmann & Franco 2009; Lawes *et al.* 2011b) despite the prevailing patterns we have shown. The recent loss of herbivores from some afro-tropical savannas may also have led to more intense fire regimes that are similar to those of the neotropics, perhaps resulting in novel selection pressures.

The fact that the *lanky* strategy dominates in afro-tropical savannas does not mean that bark thickness has no role in these ecosystems; in fact, a certain bark thickness is needed to protect the stem from low intensity fires, but the relative importance of bark thickness clearly differs between the two biogeographical regions because of the contrasting fire regimes. If we consider the nearby (less flammable) forest patches embedded in the cerrado mosaics, neo-tropical forest trees have thinner barks than neo-tropical and afro-tropical savanna trees (Fig. S1), suggesting that differences are

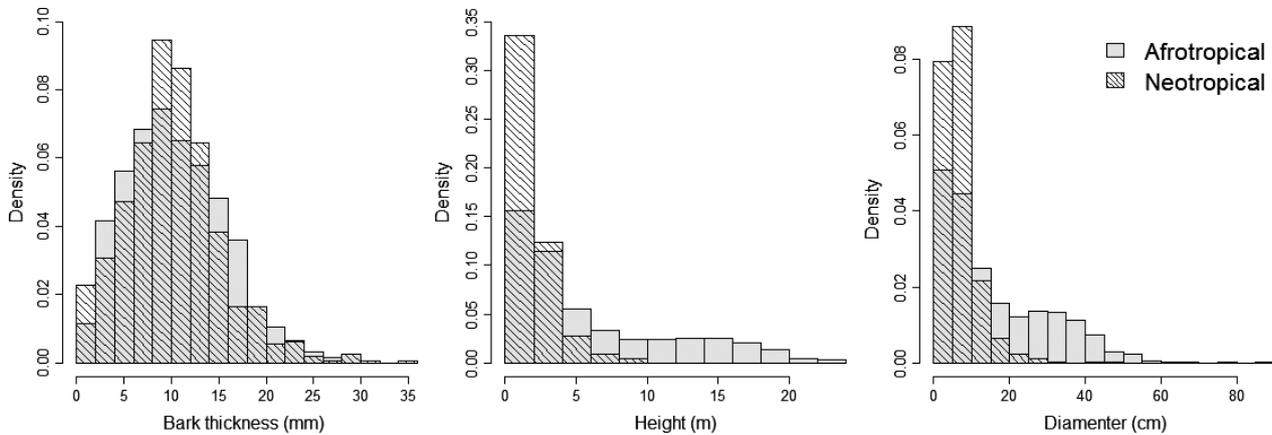


Fig. 3. Frequency distribution of bark thickness (mm), height (m) and diameter (cm) in afro-tropical (grey bars) and neo-tropical (hatching) savannas. Mean (and SD) values are for afro-tropical trees, 9.22 ± 5.85 mm (bark), 6.93 ± 5.96 m (height), 0.17 ± 0.14 m (diameter) and for neo-tropical trees, 10.09 ± 5.06 mm (bark), 1.89 ± 1.48 m (height), 0.07 ± 0.05 m (diameter). Differences between afro-tropical and neo-tropical values are not significantly different for bark thickness ($P = 0.61$) and are highly significant for height and diameter ($P < 0.0001$, Wilcoxon rank test).

Table 2. Summary of the general linear mixed model analyses testing the differences in the relationship between bark thickness (mm) and stem height (m) against diameter (m) between ecozones (afro-tropical vs. neo-tropical; see Fig. 3)

	Df	AIC	LR	P	Estimate
Bark thickness					1.58 [intercept]
log(diam)	4	-906.31			0.73 log(diam)
+Ecozone (E)	5	-967.09	62.78	<0.0001	0 [Afrotr], 0.25 [Neotr]
+log(diam) \times E	6	-967.21	2.11	ns	
Height					1.12 [intercept]
log(diam)	4	-630.78			0.61 log(diam)
+Ecozone (E)	5	-646.81	18.03	<0.0001	0 [Afrotr], -0.02 [Neotr]
+log(diam) \times E	6	-667.37	22.56	<0.0001	0.12 log(diam) [Neotr]
Height (for diam < 5 cm)					1.04 [intercept]
log(diam)	4	34.11			0.56 log(diam)
+Ecozone (E)	5	18.07	18.04	<0.0001	0 [Afrotr], -0.20 [Neotr]
+log(diam) \times E	6	19.75	0.32	ns	

The analyses correspond to plants with overlapping range sizes between afro-tropical and neo-tropical savannas (see Fig. 4); for a comparison including all data compiled see Table S5). Species were considered as random factors. Degree of freedom (Df), AIC and the likelihood ratio test (LR) are presented. For each model, the rightmost column provides the estimated parameters for the fixed effects of the final significant model. Analysis includes only the data in which the range of tree diameters overlap (see Methods).

ecological rather than biogeographical. Evidence also points out to the coexistence of the two strategies in some afro-tropical savannas (Gignoux, Clobert & Menaut 1997). Moreover, the striking differences in size between afro-tropical and neo-tropical savanna trees (larger in the former; Fig. 3) are not due to biogeographical differences, as in the Neotropics some trees have the same size or are even larger, than those in the African savannas (Fig. S1). However, because fires tend to be more intense in neo-tropical savannas, the thin barks of the *lanky* strategy provide insufficient protection (Hoffmann *et al.* 2009). Thus, development to adult size classes on these plants is often confined to protected patches of closed-canopy forests that inhibit shade-intolerant grasses and thus benefit from a considerable reduction in flammability and fire intensities (Hoffmann *et al.* 2011, 2012).

Thick barks have traditionally been associated with trees living in ecosystems with understorey fire regimes (Keeley & Zedler 1998; He *et al.* 2012). Here, we provide evidence that

thick bark is also a successful fire protection strategy in fire regimes where the entire plant is affected by fire (Fig 4; Dantas *et al.* 2013 and Dantas, Batalha & Pausas in press). Compared with typical crown-fire ecosystems, fires in neo-tropical savannas are very frequent and of relatively low intensity. In such conditions, small differences in bark thickness may provide sufficient fitness benefit to be selected. The *corky* strategies of having a thick bark along the whole stem and branches coupled with epicormic resprouting also appear in some nontropical oak woodlands where fires are frequent (Zedler 1995; Pausas 1997; Catry *et al.* 2012).

We have focused on bark thickness as a stem insulation mechanism, despite the fact that there are other stem traits that may also be relevant in reducing heat transfer, such as bark density and porosity (Lawes *et al.* 2011b), bark moisture (Midgley, Lawes & Chamaille-Jammes 2010; Lawes *et al.* 2011b; Brando *et al.* 2012; Higgins *et al.* 2012) and stem-specific density (Brando *et al.* 2012). In isolation, these

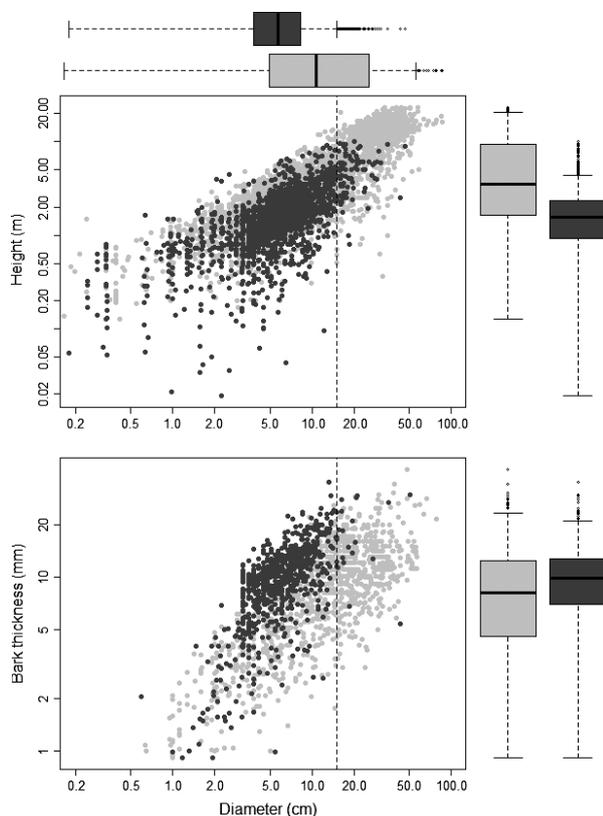


Fig. 4. Height (m, top) and bark thickness (mm, bottom) in relation to stem diameter (cm) for trees in afro-tropical savannas (grey symbols), and neo-tropical savannas (black symbols). Axes are presented in log-scale. Vertical dashed lines refer to the upper size considered for the statistical comparison (Table 2); the statistical comparison for the full data set is provided in Table S5.

traits rarely predict the probability of topkill in savanna plants (e.g. Higgins *et al.* 2012), and there is overwhelming evidence that bark thickness is the main protective bark trait in tropical ecosystems (Pinard & Huffman 1997; Hoffmann *et al.* 2009; Lawes *et al.* 2011a; Brando *et al.* 2012). Although the main path by which African savanna plants escape fire seems to be related to the *lanky* strategy (Lawes, Midgley & Clarke 2013), the interspecific variability of bark traits may also be important in predicting species abundances at local and regional scales (Higgins *et al.* 2012).

Differences between ecozones could have a phylogenetic basis as the two zones share very few clades (Tables S4 and S6). However, this is not expected, at least for bark thickness, as this trait is strongly convergent (Simon *et al.* 2009); that is, thick barks appear in many different lineages and closely related species may have differing bark thicknesses for a given diameter (Hoffmann, Orthen & Nascimento 2003). Plant height is more evolutionary conserved (Swenson & Enquist 2009; Silva & Batalha 2010; Yessoufou *et al.* 2013), although there is some evidence, at least for one shared clade (Fabaceae), that tree saplings grow faster in height in afro-tropical savannas (from 11 to 25 cm year⁻¹; Wakeling, Staver & Bond 2011) than in neo-tropical savannas (from 3.1 to 5.52 cm year⁻¹; Braz, Kanegae & Franco 2000; Kanegae, Braz & Franco 2000;

Azevedo 2006). In addition, the fact that neo-tropical closed-forest have thinner bark and are taller than the afro-tropical savannas (Fig. S1) also points out towards an ecological rather than a biogeographical or historical process.

Australian savannas are also subjected to recurrent fires and, because of the very long history of plant–fire interaction (Bond & Midgley 2001), species have evolved a variety of bud-insulating mechanisms (Burrows *et al.* 2010). Specifically, Australian eucalypts have buds embedded within the trunk (Burrows 2002) and consequently achieve stem protection with thinner barks than noneucalypt species (Lawes *et al.* 2011a). Because of this mechanism, eucalypts allocate little to bark thickness, and this enables a relatively fast growth in height (Prior *et al.* 2006). Nevertheless, the *corky* strategy is fundamental in noneucalypts of Australian mesic savannas (Lawes *et al.* 2011a; Lawes, Midgley & Clarke 2013) supporting our rationale of the importance of this strategy in mesic savannas with low herbivore densities.

While there is plenty of information about the role of fire (e.g. Keeley *et al.* 2011) and herbivory (e.g. Díaz *et al.* 2007) in shaping plant traits, their interactive effects have received little attention (Pausas & Lavorel 2003; Midgley, Lawes & Chamaillé-Jammes 2010). Savannas are a prevalent example of consumer-controlled ecosystems (Bond & Keeley 2005; Bond, Woodward & Midgley 2005), and we propose that the relative importance of the different consumers (fire and herbivory) may determine the dominant fire-escape strategy and community structure. Given that the relative role of consumers varies across the globe, our model might help to explain the contrasting strategies of savanna plants and the structure of savanna ecosystems world-wide.

Acknowledgements

The authors are grateful to the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP; process: 2010/01835-0); the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES; process: 1019-11-2); and the Spanish Government (VIRRA and TREVOL projects, CGL2009-12048/BOS and CGL2012-39938-C02-00) for financial support and the scholarships granted to the authors; Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) for research permission; Emas National Park staff for logistical assistance; M.A. Batalha, M.V. Cianciaruso, N. Escobar, P.P. Loiola, N. Rosatti, D.M. Silva, I.A. Silva for valuable help in field sampling; M.A. Batalha, M.V. Cianciaruso and I.A. Silva for helping with species identification; and E. Ribeiro for helping in the GIS analysis. The authors have no conflict of interest to declare.

References

- Archibald, S. & Bond, W.J. (2003) Growing tall vs growing wide: tree architecture and allometry of *Acacia karoo* in forest, savanna, and arid environments. *Oikos*, **102**, 3–14.
- Archibald, S., Bond, W.J., Stock, W.D. & Fairbanks, D.H.K. (2005) Shaping the landscape: fire–grazer interactions in an African savanna. *Ecological Applications*, **15**, 96–109.
- Asner, G.P., Levick, S.R., Kennedy-Bowdoin, T., Knapp, D.E., Emerson, R., Jacobson, J., Colgan, M.S. & Martin, R.E. (2009) Large-scale impacts of herbivores on the structural diversity of African savannas. *Proceeding of the National Academy of Science*, **106**, 4947–4952.
- Azevedo, I.N.C. (2006) *Regeneração e estabelecimento de Copaifera longsdorffii (Desf.) e Emmotum nitens (Benth.) Miers em condições naturais*. MSc Dissertation, Universidade de Brasília, Brasília.

- Bond, W.J. (2008) What limits trees in C 4 grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics*, **39**, 641–659.
- Bond, W.J., Cook, G.D. & Williams, R.J. (2012) Which trees dominate in savannas? The escape hypothesis and eucalypts in northern Australia. *Austral Ecology*, **37**, 678–685.
- Bond, W.J. & Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, **20**, 387–395.
- Bond, W.J. & Midgley, J.J. (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution*, **16**, 45–51.
- Bond, W.J., Smythe, K.-A. & Balfour, D.A. (2008) Acacia species turnover in space and time in an African savanna. *Journal of Biogeography*, **28**, 117–128.
- Bond, W.J. & van Wilgen, B.W. (1996) *Fire and Plants*. Chapman & Hall, London.
- Bond, W.J., Woodward, F.I. & Midgley, J.F. (2005) The global distribution of ecosystems in a world without fire. *New Phytologist*, **165**, 525–538.
- Brando, P.M., Nepstad, D.C., Balch, J.K., Bolker, B., Christman, M.C., Coe, M. & Putz, F.E. (2012) Fire-induced tree mortality in a neotropical forest: the roles of bark thickness, tree size, woody density and fire behavior. *Global Change Biology*, **18**, 630–641.
- Braz, V.S., Kanegae, M.F. & Franco, A.C. (2000) Estabelecimento e desenvolvimento de *Dalbergia miscolobium* benth. Em duas fitofisionomias típicas dos cerrados do Brasil central. *Acta Botanica Brasílica*, **14**, 27–35.
- Burrows, G.E. (2002) Epicormic strand structure in *Angophora*, *Eucalyptus* and *Lophostemon* (Myrtaceae) – implications for fire resistance and recovery. *New Phytologist*, **153**, 111–131.
- Burrows, G.E., Hornby, S.K., Waters, D.A., Bellairs, S.M., Prior, L.D. & Bowman, D.M.J.S. (2010) A wide diversity of epicormic structures is present in Myrtaceae species in the northern Australian savanna biome – implications for adaptation to fire. *Australian Journal of Botany*, **58**, 493–507.
- Catry, F.X., Moreira, F., Pausas, J.G., Fernandes, P.M., Rego, F., Cardillo, E. & Curt, T. (2012) Cork oak vulnerability to fire: the role of bark harvesting, tree characteristics and abiotic factors. *PLoS One*, **7**, e39810.
- Costa, A.N., Vasconcelos, H.L., Vieira-Neto, E.H.M. & Bruna, E.M. (2008) Do herbivores exert top-down effects in Neotropical savannas? Estimates of biomass consumption by leaf-cutter ants. *Journal of Vegetation Science*, **19**, 849–854.
- Dantas, V.L., Batalha, M.A. & Pausas, J.G. (2013) Fire drives functional thresholds on the savanna-forest transition. *Ecology*, doi: 10.1890/12-1629.1.
- Dantas, V.L., Pausas, J.G., Batalha, M.A., Loiola, P.P. & Cianciaruso, M.V. (2013) The role of fire in structuring trait variability in Neotropical savannas. *Oecologia*, **171**, 487–494.
- Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D. G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H. & Campbell, B. D. (2007) Plant trait responses to grazing – a global synthesis. *Global Change Biology*, **13**, 313–341.
- Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M. & Collins, S.L. (2003) Productivity responses to altered rainfall patterns in a C₄-dominated grassland. *Oecologia*, **137**, 245–251.
- Fuhlendorf, S.D., Engle, D.M., Kerby, J. & Hamilton, R. (2008) Pyric herbivory: rewinding landscapes through the recoupling of fire and grazing. *Conservation Biology*, **23**, 588–598.
- Gignoux, J., Clobert, J. & Menaut, J.-C. (1997) Alternative fire resistance strategies in savanna trees. *Oecologia*, **110**, 576–583.
- Gill, A.M. & Ashton, D.H. (1968) The role of bark type in relative tolerance to fire of the three central Victorian eucalypts. *Australian Journal of Botany*, **16**, 491–498.
- Grace, J., San José, J., Meir, P., Miranda, H.S. & Montes, R.A. (2006) Productivity and carbon fluxes of tropical savannas. *Journal of Biogeography*, **33**, 387–400.
- He, T., Pausas, J.G., Belcher, C.M., Schwilk, D.W. & Lamont, B.B. (2012) Fire-adapted traits of *Pinus* arose in the fiery Cretaceous. *New Phytologist*, **194**, 751–759.
- Higgins, S.I., Bond, W.J. & Trollope, W.S.W. (2000) Fire, resprouting and variability: a recipe for tree-grass coexistence in savanna. *Journal of Ecology*, **88**, 213–229.
- Higgins, S.I., Bond, W.J., February, E.C., Bronn, A., Euston-Brown, D.I.W., Enslin, B. *et al.* (2007) Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology*, **88**, 1119–1125.
- Higgins, S.I., Bond, W.J., Combrink, H., Craine, J.M., February, E.C., Govender, N., Lannas, K., Moncreiff, G. & Trollope, W.S.W. (2012) Which traits determine shifts in the abundance of tree species in a fire-prone savanna? *Journal of Ecology*, **100**, 1400–1410.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Hoffmann, W.A., Orthen, B. & Nascimento, P.K.V. (2003) Comparative fire ecology of tropical savanna and forest trees. *Functional Ecology*, **17**, 720–726.
- Hoffmann, W.A., Dasmé, R.A., Haridasan, M., Carvalho, M.T., Geiger, E.L., Pereira, M.A.B., Gotsch, S.G. & Franco, A.C. (2009) Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. *Ecology*, **90**, 1326–1337.
- Hoffmann, W.A., Jaconis, S.Y., McKinley, K.L., Geiger, E.L., Gotsch, S.G. & Franco, A.C. (2011) Fuels or microclimate? Understanding the drivers of fire feedbacks at savanna-forest boundaries. *Austral Ecology*, **37**, 634–643.
- Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L., Haridasan, M. & Franco, A.C. (2012) Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters*, **5**, 759–768.
- Kanegae, M.F., Braz, V.S. & Franco, A.C. (2000) Efeitos da seca sazonal e disponibilidade de luz na sobrevivência e crescimento de *Bowdichia virgilioides* em duas fitofisionomias típicas dos cerrados do Brasil Central. *Revista Brasileira de Botânica*, **23**, 459–468.
- Keeley, J.E. & Zedler, P.H. (1998) Evolution of life histories in *Pinus*. *Ecology and biogeography of Pinus* (ed. D. M. Richardson), pp. 219–249. Cambridge University Press, Cambridge.
- Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J. & Bradstock, R.A. (2011) Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, **16**, 406–411.
- Köppen, W. (1931) *Grundriss der Klimakunde*. W. de Gruyter, Berlin.
- Lawes, M.J., Midgley, J.J. & Clarke, P.J. (2013) Costs and benefits of relative bark thickness in relation to fire damage: a savanna/forest contrast. *Journal of Ecology*, **101**, 517–524.
- Lawes, M.J., Adie, H., Russell-Smith, J., Murphy, B. & Midgley, J. (2011a) How do small savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark thickness. *Ecosphere*, **2**, art42.
- Lawes, M.J., Richards, A., Dathé, J. & Midgley, J.J. (2011b) Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant Ecology*, **212**, 2057–2069.
- Lehmann, C.E.R., Archibald, S.A., Hoffmann, W.A. & Bond, W.J. (2011) Deciphering the distribution of the savanna biome. *New Phytologist*, **191**, 197–209.
- Marquis, R.J., Diniz, I.R. & Morais, H.C. (2001) Patterns and correlates of interspecific variation in foliar insect herbivory and pathogen attack in Brazilian cerrado. *Biotropica*, **17**, 127–148.
- Medeiros, M.B. & Miranda, H.S. (2008) Post-fire resprouting and mortality in cerrado woody plant species over a three-year period. *Edinburgh Journal of Botany*, **65**, 53–68.
- Midgley, J.J., Lawes, M.J. & Chamaillé-Jammes, S. (2010) Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Australian Journal of Botany*, **58**, 1–11.
- Moncreiff, G.R., Chamaillé-Jammes, S., Higgins, S., O'Hara, R.B. & Bond, W.J. (2011) Tree allometries reflect a lifetime of herbivory in an African savanna. *Ecology*, **92**, 2310–2315.
- Murphy, B.T. & Bowman, D.M.J.S. (2012) What controls the distribution of tropical forest and savanna? *Ecology Letters*, **15**, 748–758.
- Pausas, J.G. (1997) Resprouting of *Quercus suber* in NE Spain after fire. *Journal of Vegetation Science*, **8**, 703–706.
- Pausas, J.G. & Lavorel, S. (2003) A hierarchical deductive approach for functional types in disturbed ecosystems. *Journal of Vegetation Science*, **14**, 409–416.
- Pausas, J.G. & Ribeiro, E. (2013) The global fire-productivity relationship. *Global Ecology and Biogeography*, **22**, 728–736.
- Pinard, M.A. & Huffman, J. (1997) Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. *Journal of Tropical Ecology*, **13**, 727–740.
- Prior, L.D., Brook, B.W., Williams, R.J., Werner, P.A., Bradshaw, C.J.A. & Bowman, D.M.J.S. (2006) Environmental and allometric drivers of tree growth rates in a north Australian savanna. *Forest Ecology and Management*, **234**, 164–180.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Wien, AT, USA.
- Rohatgi, A. (2012) *WebPlotDigitalizer: HTML5 based online tool to extract numerical data from plot images*. Version 3. [WWW document] URL <http://arohatgi.info/WebPlotDigitizer/app/> (accessed on November 2012).

- Rossatto, D.R., Hoffmann, W.A. & Franco, A.C. (2009) Differences in growth patterns between co-occurring forest and savanna species affect the forest-savanna boundary. *Functional Ecology*, **23**, 689–698.
- Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S. *et al.* (2005) Determinants of woody cover in African savannas. *Nature*, **438**, 846–849.
- Savadogo, P., Zida, D., Sawadogo, L., Tiveau, D., Tigabu, M. & Odén, P.C. (2007) Fuel and fire characteristics in savanna-woodland of West Africa in relation to grazing and dominant grass type. *International Journal of Wildland Fire*, **16**, 531–539.
- Scogings, P.F., Mamashela, T.C. & Zobolo, A.M. (2012) Deciduous sapling responses to season and large herbivores in a semi-arid African savanna. *Austral Ecology*, **38**, 548–556.
- Silva, I.A. & Batalha, M.A. (2010) Woody plant species co-occurrence in Brazilian savannas under different fire frequencies. *Acta Oecologica*, **36**, 85–91.
- Simon, M.F., Grether, R., Queiroz, L.P., Skema, C., Pennington, R.T. & Hughes, C.E. (2009) Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Science USA*, **106**, 20359–20364.
- Staver, A.C., Bond, W.J., Stock, W.D., Van Rensburg, S.J. & Waldram, M.S. (2009) Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications*, **19**, 1909–1919.
- Swenson, N.G. & Enquist, B.J. (2009) Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology*, **90**, 2161–2170.
- Vines, R.G. (1968) Heat transfer through bark, and the resistance of trees to fire. *Australian Journal of Botany*, **16**, 499–514.
- Wakeling, J.L., Staver, A.C. & Bond, W.J. (2011) Simply the best: the transition of savanna saplings to trees. *Oikos*, **120**, 1448–1451.
- Wooster, M.J., Zhukov, B. & Oertel, D. (2003) Fire radiative energy for quantitative study of biomass burning: derivation from the BIRD experimental satellite and comparison to MODIS fire products. *Remote Sensing of Environment*, **86**, 83–107.
- Yessoufou, K., Davies, T.J., Maurin, O., Kuzmina, M., Schaefer, H., van der Bank, M. & Savolainen, V. (2013) Large herbivores favour species diversity but have mixed impacts on phylogenetic community structure in an African savanna ecosystem. *Journal of Ecology*, **101**, 614–625.
- Zedler, P.H. (1995) Are some plants born to burn? *Trends in Ecology and Evolution*, **10**, 393–395.

Received 10 February 2013; accepted 16 May 2013

Handling Editor: Peter Bellingham

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Reference sources for the information in Table 1.

Table S2. Data compiled for afro-tropical and neotropical savannas.

Table S3. Available information on the study sites from which the data was compiled.

Table S4. List of the species used in this study.

Table S5. Summary of the general linear mixed model analyses testing the differences in the relationship between bark thickness and stem height against diameter between ecozones using the entire data set.

Table S6. Shared families and the numbers of species within them for each trait (Bark thickness or height vs. diameter) and ecoregion (afrotropical and neotropical).

Figure S1. Height and bark thickness in relation to stem diameter for afrotropical savanna, neotropical savanna, and neotropical closed-forest trees.