Letters

Bark thickness and fire regime: another twist

A comment on Rosell (2016) 'Bark thickness across the angiosperms: more than just fire'

Bark is the outermost covering of stems in woody plants and plays a fundamental protective role. Recently I hypothesized that 'at the global scale, a significant proportion of the variability in bark thickness is explained by the variability in fire regimes', and specifically predicted that frequent low intensity fires select for thick bark (Pausas, 2015). In addition, I suggested that differentiating between inner and outer bark thickness would help us gain a better understanding of the functional role of bark, especially in nonfire prone ecosystems. Based on an understanding of the selection pressure by fire and on other plant traits, I showed that some fire regimes select for thick bark at the base of the trunk, others select thick bark on the whole plant (stem, branches, twigs), while other fire regimes do not select for thick bark – and thus relatively thin barks are the more likely to be observed (Table 1). However, the paucity of available data at a global scale limited an empirical demonstration of the proposed framework.

A new paper has now provided evidence for the fire hypothesis of bark thickness at a global scale. Rosell (2016) sampled bark thickness in woody species from 18 sites in different climates and fire regimes, and has demonstrated that fire regime was the main environmental factor explaining variability in bark thickness (after accounting for plant size; Fig. 1). But perhaps the most valuable contribution of Rosell is that, in addition to total bark thickness, she accurately measured inner and outer bark thickness, and showed that they behave differently: the role of fire is especially relevant for explaining outer bark thickness (Fig. 1; see Schafer *et al.*, 2015, for similar results), while inner bark does not seem to provide protection for the cambium from heat. This provides a step forward in our understanding of the ecology of bark. These results were found despite the relatively simple estimation of fire regime (semiquantitative fire frequency, 1–5), compared with alternative parameters (climate) that were more precise and variable. This simple estimation of fire regime is understandable as fire history is not as available as climate data (remotely-sensed fire activity could be a possible source; Pausas & Ribeiro, 2013). Below I take the opportunity to comment on how we could advance our understanding of the role of fire in shaping bark thickness by considering more detailed fire regime information coupled with some plant life-history traits.

Fire regime is the complex combination of fire characteristics that prevails in a given area, and includes frequency, intensity, seasonality and type of fuels consumed (Keeley *et al.*, 2012). For its relevance in relation to the bark, I will focus on first fire frequency, defined as the fire return interval in relation to plant longevity; and second on the fire intensity, defined as the flame height in relation to the height of canopy fuels. The latter variable defines two very contrasted fire regimes: understory (or surface) fires (i.e. when the flame height is lower than the overstory; crowns are not consumed by the fire) and crown fires (otherwise). This distinction is important because the predictions of bark thickness differ in these two fire regimes (Table 1), and the linear expectation of bark thickness and fire frequency may not apply when mixing understory and crown fire regimes. In fact, Rosell showed that Mediterranean ecosystems have thin barks despite frequent fires; this is exactly the prediction for those ecosystems as they are subject to frequent crown fires (Table 1; Fig. 3 in Pausas, 2015). Stating that fire regimes explain an important part of the variability in bark thickness does not mean that bark thickness and fire frequency should show a strong positive correlation; for example, the high frequency of understory fires selects for thick basal bark in trees but not in the coexisting understory plants; and the high frequency of crown fires does not select for thick bark at all (Keeley & Zedler, 1998; Pausas, 2015). In fact, I expect bark thickness to be related to the frequency of low intensity fires (Pausas, 2015). When Rosell analysed her data separating short (< 2 m) and tall (> 2 m) species, the effect of fire on bark thickness disappears in the former and increases in the latter (Fig. 1). This is probably because many of the short species grow in shrublands subject to crown fires or are in the understorey of forests; in such cases thin barks are expected

Table 1 Predicted total bark thickness in relation to the fire regime (Pausas, 2015)

Fire regime	Examples	Prediction of bark thickness
Frequent surface fires in forests and woodlands (A)	Southern North American pine forests	Trees with thick basal bark, understory shrubs with thin bark
Frequent grass-fuelled surface fires in open ecosystems (B)	African savannas	Trees with moderate bark thickness
Frequent tall grass-fuelled fires affecting crowns (C)	Brazilian savannas (cerrado)	Trees and shrubs with thick bark in the stem and branches
Frequent high-intensity, woody-fuelled crown fires in forests and shrublands (D)	Mediterranean shrublands	Thin bark
Infrequent drought-driven high-severity fires (E)	Rainforests, cold temperate forests	Thin bark
Infrequent fuel-limited fires (F)	Arid ecosystems	Variable

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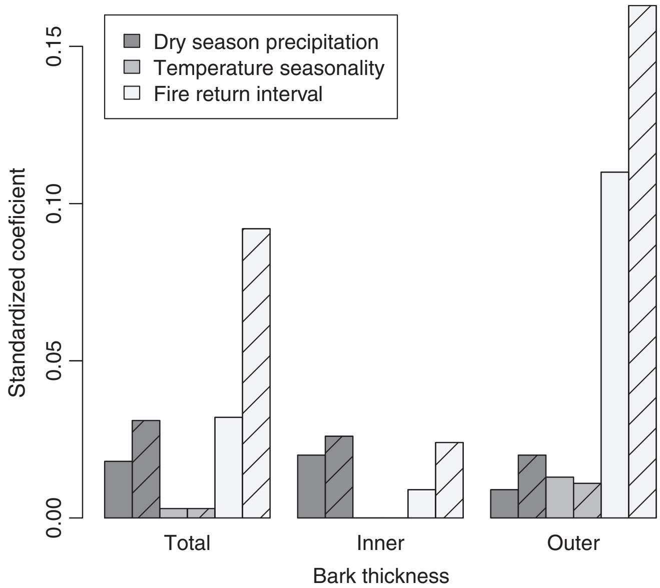

Fig. 1 Relative role of climate (dry season precipitation and temperature seasonality) and fire (fire return interval) in determining bark thickness (total, inner, outer bark thickness) based on *c.* 500 species from 18 communities distributed worldwide (Australia, Brazil, California (USA), Italy and Mexico). Values are the squared standardized coefficients of multiple regression models after accounting for stem diameter (from Rosell, 2016). Climatic data were quantitative (in millimetres and °C), fire regime data were semiquantitative (1–5). Bars with stripes refer to the results when the analysis is restricted to species taller than 2 m.

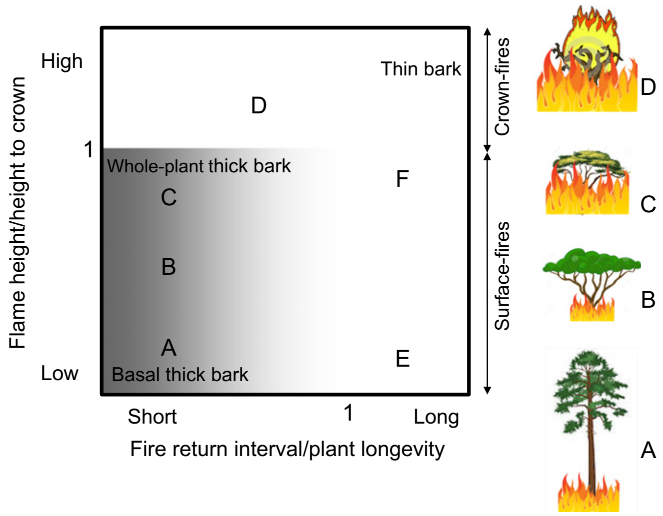

Fig. 2 Bark thickness as a function of fire regime: flame height (an indicator of fire intensity) and mean fire return interval (fire frequency). Fire regime is scaled by the characteristics of the plant (height to the base of the crown and longevity, respectively). The shaded area represents the areas where thick barks are adaptive for fire protection, that is, when return intervals are shorter than the lifespan of the plant and fires are of low intensity (flame height is shorter than the distance to the base of the crown, e.g. surface fires); the shaded area is limited by thresholds (values of 1 on the axes). The unshaded area represents the conditions where thick barks are not adaptive (thin bark is more likely), that is, when fires are crown-fires or when the return interval is long (in relation to the longevity of the plant). Letters A–F represent the approximate location of the dominant woody species of the six fire regimes in Table 1, and the drawings on the right illustrate the scenarios A–D.

(Table 1); by contrast, trees taller than 2 m may include a wide variability of conditions (from trees in fire-free wet forests to trees under surface fire regimes where thick bark is expected). Therefore, the results of splitting species by growth form are also congruent with the predictions and further support the role of fire in shaping bark thickness (Pausas, 2015).

These results suggest that to understand bark thickness it is necessary to account for different fire regime components coupled by some plant traits (Fig. 2). A thick fire-protective bark is expected when fire return intervals are shorter than the lifespan of the plant, and the flame height is shorter than the height of the base of the canopy (i.e. when there is a gap between surface fuels and canopy fuels; e.g. surface or understory fires). The same fire frequency may select for thick bark where the flame is small in relation to the plant (surface fires in forests), or for thin bark where the flame burns the canopy (i.e. crown fires like those occurring in the Mediterranean shrublands). In fact, we would expect a thicker bark in relation to the stem diameter as the flame height increases (in relation to the canopy height) in low intensity fire regions (grass-fuelled surface-fires – the grey area in Fig. 2). In an ecosystem with long fire intervals, a thick bark may still be relevant but for only the long-lived plants; this may explain the occurrence of bark protected plants in some arid ecosystems (Cousins *et al.*, 2016; Schubert *et al.*, 2016), and the high variability of bark thickness in these ecosystems (Table 1). However, the variability in bark thickness of most species in arid ecosystems may be shaped by factors other than fire (such as water control or structural stability; see Paine *et al.*, 2010; Rosell *et al.*, 2014; Pausas, 2015; Richardson *et al.*, 2015). To what extent these patterns (Fig. 2) are driven by the outer bark only remains unknown, but the research by Rosell points in that direction. Validating the model in Fig. 2 may not be easy, but it does show that a linear relation between fire frequency and bark thickness is not necessarily the expectation; thresholds do exist. In any case, I hope it may help to redefine further research in this topic.

Bark thickness is a key trait structuring many woody plant communities in ecosystems subject to fire. It is especially relevant in tropical ecosystems where there is a bark thickness threshold that allows the plant to enter frequently burnt communities (Hoffmann *et al.*, 2012); consequently, average bark thickness is strongly associated with fire regime and with many other community attributes (e.g. forest–savanna transitions; Dantas *et al.*, 2013). Thin-barked trees enter in the community when fire intervals are long, as can be observed in ecosystems subjected to strong fire exclusion regimes (Harmon, 1984; Gilliam & Platt, 1999; Peterson & Reich, 2001). Thus, intra-site variability is expected in transition zones and very dynamic systems or where plant longevity is very variable (Fig. 2). In addition, thin- and thick-barked plants can coexist under a given fire regime because there are alternative mechanisms for fire survival, such as other stem-protective mechanisms different from having a thick bark (e.g. Burrows, 2002; Gagnon *et al.*, 2010), or moving buds underground (e.g. Maurin *et al.*, 2014; Paula *et al.*, 2016). This is especially relevant in highly diverse ecosystems where different lineages may have evolved different ‘solutions’ to a given ‘problem’. That is, not all species in a given fire regime may have acquired a thick bark, just as not all species living in grazing systems have evolved thorns.

Overall, fire regime is not expected to explain 100% of the variance of bark thickness, even in fire-prone ecosystems; but it does explain a very important proportion of the variance – especially when the different components of fire regimes are taken into account (see Fig. 2). The work by Rosell, when framed in relation to the selection processes of bark thickness, represents a step forward in understanding the ecology of bark at a global scale, and on the relative role of fire in shaping bark thickness. Thus, we are gaining a more complete understanding of stem defence strategies in plants.

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