

REVIEWS AND SYNTHESES

Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes

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Abstract

Fire shapes the distribution of savanna and forest through complex interactions involving climate, resources and species traits. Based on data from central Brazil, we propose that these interactions are governed by two critical thresholds. The *fire-resistance threshold* is reached when individual trees have accumulated sufficient bark to avoid stem death, whereas the *fire-suppression threshold* is reached when an ecosystem has sufficient canopy cover to suppress fire by excluding grasses. Surpassing either threshold is dependent upon long fire-free intervals, which are rare in mesic savanna. On high-resource sites, the thresholds are reached quickly, increasing the probability that savanna switches to forest, whereas low-resource sites are likely to remain as savanna even if fire is infrequent. Species traits influence both thresholds; saplings of savanna trees accumulate bark thickness more quickly than forest trees, and are more likely to become fire resistant during fire-free intervals. Forest trees accumulate leaf area more rapidly than savanna trees, thereby accelerating the transition to forest. Thus, multiple factors interact with fire to determine the distribution of savanna and forest by influencing the time needed to reach these thresholds. Future work should decipher multiple environmental controls over the rates of tree growth and canopy closure in savanna.

Keywords

Alternate stable states, critical thresholds, forest, savanna, tipping point.

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INTRODUCTION

Understanding the factors that govern the distribution of tropical forest and savanna has important implications for managing savanna ecosystems, elucidating the origin of the savanna biome and projecting the response of tropical landscapes to changing climate and disturbance regimes. Unfortunately, there is no consensus regarding the relative importance of climate, fire, hydrology, herbivory and soil characteristics in mediating the balance between these biomes (e.g. Tinley 1982; Hopkins 1992; Ruggiero *et al.* 2002; Hirota *et al.* 2010; Good & Caylor 2011). Of the multiple factors that limit tree success in savanna, fire appears to be the most widespread and universal in savannas worldwide (Bond 2008; Staver *et al.* 2011b); therefore, it is doubtful that the distribution of savanna and forest can be adequately explained without explicitly considering the role of fire.

The strongest evidence for an overriding role of fire comes from observations of savannas subjected to fire suppression. Throughout mesic savanna regions (i.e. where mean annual precipitation > 800 mm), there are ample observations of forest encroachment into savanna upon long-term fire suppression (Hopkins & Jenkin

1962; San José & Fariñas 1991; Hopkins 1992; Ratter 1992; Swaine *et al.* 1992; Bowman *et al.* 2001; Durigan & Ratter 2006; Pinheiro *et al.* 2010). In drier savannas, climate alone may prevent the development of a closed forest canopy (Sankaran *et al.* 2005; Good & Caylor 2011), but this does not appear true of mesic savanna regions (Bond *et al.* 2005; Sankaran *et al.* 2005; Lehmann *et al.* 2011; Staver *et al.* 2011a). In these relatively wet regions, insufficient nutrient stocks can sometimes pose an absolute constraint on tree density, but this does not appear to be widespread (Bond 2010). Locally, other edaphic factors, such as shallow, sandy or seasonally flooded soils, might prevent some sites from ever becoming forest during fire suppression, but cannot explain the existence of savanna on well-drained clay soils that are widespread throughout the seasonal tropics. But most tellingly, widespread observations of forest encroachment under fire suppression leave little doubt that extensive areas now dominated by savanna have the potential to become forest. The persistence of savanna in these areas is dependent on fire or other disturbance to prevent canopy closure.

In the absence of fire, the increase in tree density is a gradual process involving recruitment of new trees as well as growth of

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existing stems. Fire interrupts this process by reducing the size of existing trees through topkill (i.e. loss of above-ground biomass), combined with a small amount of whole-plant mortality (Williams *et al.* 1999; Hoffmann & Solbrig 2003; Holdo 2005; Higgins *et al.* 2007). Other processes such as drought and herbivory may reduce tree cover in an analogous manner to fire, but are much less ubiquitous. Whereas drought-induced tree mortality is an occasional event in some xeric savannas, it is much less widely observed in mesic savannas (Fensham *et al.* 2009). Browsers can have large impacts on tree density in Africa (Asner *et al.* 2009; Midgley *et al.* 2010), but are absent from the savannas of Australia and South America.

In very general terms, the factors that govern tree density within savanna are likely to also govern the distribution of savanna and forest biomes. It is important, however, to recognise that the transition between savanna and forest differs fundamentally in two regards from gradients of tree density that are commonly observed within savanna environments. First, the tree species that dominate forest habitats are distinct from those typical of savanna environments (Bowman 2000; Hoffmann *et al.* 2009; Ratnam *et al.* 2011), and possess a different suite of species traits that must be considered if we are to understand ecosystem properties and vegetation responses to fire (Hoffmann *et al.* 2005, 2009; Gotsch *et al.* 2010). Second, forest is markedly less flammable than savanna, due to the closed canopy that excludes savanna grasses and ameliorates the understory microclimate (Biddulph & Kellman 1998; Hennenberg *et al.* 2006; Hoffmann *et al.* 2011). The succession from highly flammable savanna to non-flammable forest, therefore, results in a fundamental transition in the behaviour of the system.

The transition from savanna to forest shares many common elements with an analogous transition that occurs when an individual tree stem reaches a fire-resistant size and is no longer susceptible to topkill. As we review in this article, both transitions mark a change from (1) a state maintained by regular fire to (2) a state that is largely uninfluenced by fire. We argue that identifying the transition from one state to another provides a foundation for understanding how fire interacts with other factors to govern the distribution of savanna and forest. Finally, we use our understanding of these transitions to demonstrate the distinct roles played by savanna and forest tree species in mediating the response of these biomes to fire. This synthesis is based primarily on results from our work in the Cerrado region of Brazil.

The Cerrado is a region of approximately 2×10^6 km² dominated by mesic savanna. Most of the region receives 1000–1800 mm of rainfall annually but is marked by a dry season of 4–6 months. The Cerrado is bounded by the Amazonian and Atlantic forests and is interspersed with evergreen gallery forests along streams and upland forest types ranging from evergreen to deciduous. Savanna and grassland occur predominantly on soils with extremely low levels of available P and exchangeable bases, and locally may be subject to additional edaphic limitations, such as seasonal flooding (Amorim & Batalha 2007), a shallow hardpan or rocky or sandy soils (Pinheiro *et al.* 2010). Upland forests are often associated with soils of relatively high nutrient status, but this is not always the case, particularly for cerrado (Haridasan 1992), a forest type characterized by a mix of savanna and forest tree species (Pinheiro & Monteiro 2006).

Although most of the cerrado is subjected to regular burning, fire suppression has locally resulted in succession to cerrado forest (Durigan & Ratter 2006; Pinheiro *et al.* 2010) or expansion of forest boundaries into savanna (Ratter 1992). We have been working near Brasília,

DF, Brazil, at the IBGE Ecological Reserve, comprised predominantly of savanna vegetation with gallery forests along streams and small patches of upland cerrado forest. Fire has been actively suppressed at the site for nearly four decades, resulting in a gradual increase in the density of savanna tree species and an ingression of forest tree species into savanna. This has offered the opportunity to study the dynamics of forest expansion and to quantify the ecological, physiological and morphological differences between savanna and forest species when growing under similar environmental conditions.

CRITICAL THRESHOLDS FOR SAVANNA–FOREST DYNAMICS

In savanna, the role of fire in tree dynamics is fundamentally different from that in many other flammable ecosystems, due primarily to the presence of a continuous grass layer that regains its flammability very quickly after burning. Because of the resulting high fire frequency, juveniles of woody plants regularly undergo complete loss of aerial biomass (topkill), and thus their persistence in savanna requires the ability to resprout repeatedly (Bond & Midgley 2001). These saplings may persist for decades in a suppressed state due to repeated topkill (Higgins *et al.* 2007), whereas saplings that lack the ability to resprout repeatedly are eliminated under frequent fire (Fensham *et al.* 2003).

This suppression of juveniles by repeated topkill results in a demographic bottleneck (Fig. 1a), often referred to as a ‘fire trap’ (after Bell 1984). As long as a sapling remains suppressed by frequent topkill, it will not contribute substantially to tree cover (Hoffmann 1999; Higgins *et al.* 2000) or sexual reproduction (Hoffmann & Solbrig 2003). Recruitment into an adult size class is possible only if the sapling experiences a fire-free interval of sufficient duration to allow it to reach a critical size at which it is no longer susceptible to topkill (Bond & Midgley 2000). This size at which the tree becomes resistant to topkill will be referred to here as the *fire-resistance threshold*. Once a stem has surpassed this threshold, it is much less likely to be topkilled by subsequent fires and, therefore, can continue to grow and contribute substantially to woody cover.

An analogous threshold occurs at the ecosystem level when tree cover reaches sufficient density to reduce flammability greatly (Fig. 1b). The high fire frequency typical of mesic savanna maintains the canopy in an open state that allows highly flammable, but shade-intolerant, C₄ grasses to persist, maintaining it in a ‘landscape fire trap’ (Lindenmayer *et al.* 2011). Tropical forest, on the contrary, is much less flammable (Uhl & Kauffman 1990; Ray *et al.* 2005; Hoffmann *et al.* 2011) and generally burns much less frequently and less intensely, allowing it to maintain a dense canopy with distinct ecosystem properties (Eldridge *et al.* 2011). Savanna and forest have, therefore, been frequently regarded to represent alternate stable states maintained by the positive feedback between fire and vegetation (Wilson & Agnew 1992; Hennenberg *et al.* 2006; Beckage *et al.* 2009; Hoffmann *et al.* 2009; Warman & Moles 2009; Staver *et al.* 2011b). The point that marks the transition from highly flammable savanna to much less flammable forest will be referred to as the *fire-suppression threshold*.

Both thresholds represent a switch from a state maintained by frequent fire to a state that is not strongly influenced by fire. Once either threshold is surpassed, a return to the pre-threshold state should become increasingly dependent on extreme events. Once a stem has passed the fire-resistance threshold, the probability of topkill will decline as the stem grows and accumulates more bark. Even so, extremely intense fires can cause some topkill of large trees that would otherwise be fire resistant (Williams *et al.* 1999; Ryan & Williams 2011).

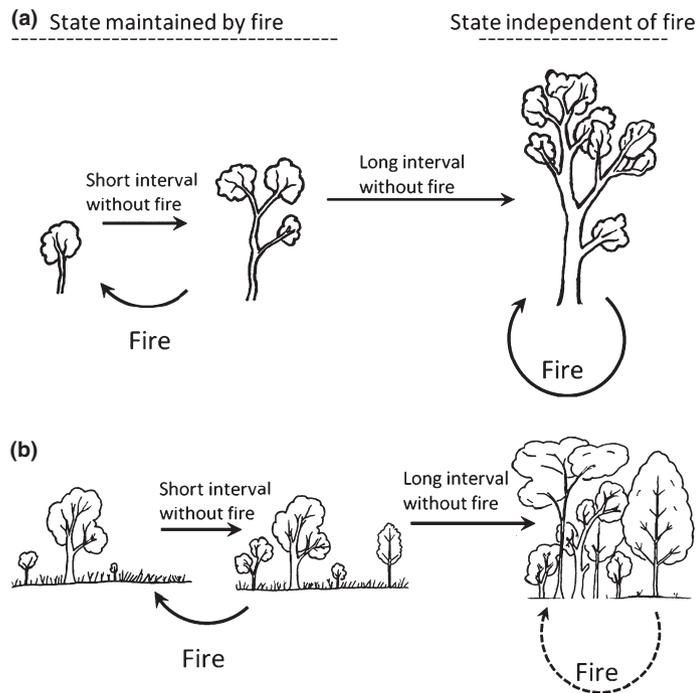


Figure 1 The two critical thresholds that govern the response of savanna systems to fire. (a) The fire-resistance threshold. Under short fire intervals, a sapling is unable to reach a fire-resistant size, and is maintained in a suppressed state by repeated episodes of topkill and resprouting. During a long fire-return interval, a stem may reach a fire-resistant size which is not topkilled by subsequent fires. (b) The fire-suppression threshold. When fire intervals are short, vegetation is maintained in an open, highly flammable state. A long fire-return interval allows canopy closure due to growth of existing trees and ingress of forest tree species. The resulting loss of grasses and change in microclimate greatly reduce flammability, hence the vegetation is largely unaffected by subsequent fires.

At the ecosystem level, once the fire-suppression threshold has been reached, subsequent fires will generally be less frequent, less intense and restricted to times of severe drought. Although low-intensity fires can be devastating in humid rainforest (Cochrane & Schulze 1999; Barlow & Peres 2008), forests of the seasonal tropics appear much more resilient to fire (Hoffmann *et al.* 2009; Balch *et al.* 2011); therefore, the return to a savanna state probably requires multiple burns to cause successive reduction in tree cover and a gradual expansion of grasses.

The fire-resistance threshold acts at the scale of individual trees, whereas the fire-suppression threshold acts at the scale of the ecosystem. Although the two thresholds are strongly interdependent, each does not necessitate the other. For example vegetation can reach a fire-suppressive state even when comprised of stems that are not fire resistant (Stevens & Beckage 2009), while open, highly flammable savannas commonly contain abundant fire-resistant trees. Nevertheless, dynamics at each scale has important consequences for the other, since large, fire-resistant trees can make substantial contributions to canopy cover, and ecosystem flammability determines whether saplings will be exposed to the risk of topkill.

QUANTIFYING THE THRESHOLDS

To understand tree dynamics in savanna, it is important to identify the points at which the fire-resistance and fire-suppression

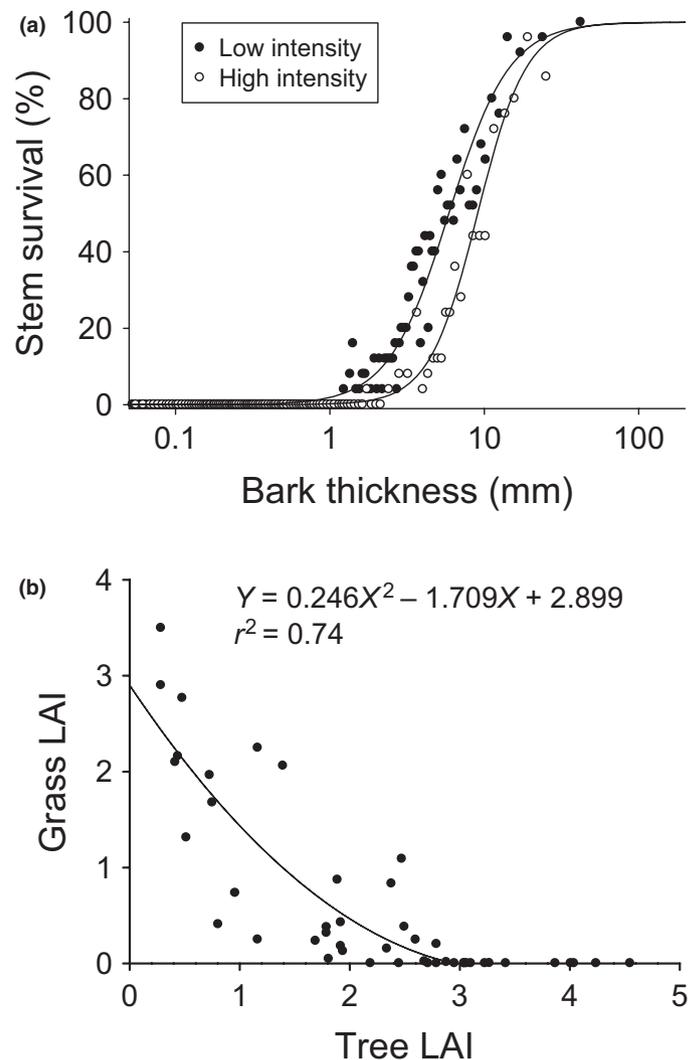


Figure 2 Critical thresholds in fire ecology of savannas. (a) Relationship between bark thickness and probability of avoiding topkill, compiled from 56 species and 15 burns (Hoffmann & Solbrig 2003; Hoffmann *et al.* 2009). A stem must accumulate a bark thickness of 5.9 mm to have a 50% chance of avoiding topkill in low-intensity fires or 9.1 mm in high-intensity fires. Bark thickness was measured at 30 cm from the ground. Each point represents the mean for 25 individuals. Low-intensity burns had flame length or char height ≤ 2 m. (b). Relationship between canopy leaf area index (LAI) and grass LAI (live and dead), compiled from Hoffmann *et al.* (2005), Silva *et al.* (2008, 2010) and Geiger *et al.* (2011).

thresholds are surpassed. Within a species, stem diameter or height can be strong predictors of topkill probability (Williams *et al.* 1999; Hoffmann & Solbrig 2003; Holdo 2005; Ryan & Williams 2011) and, therefore, can be used to define whether fire resistance is attained (e.g. Bond & Midgley 2000). When comparing species, however, stem size cannot account for the higher susceptibility of thin-barked species to topkill (e.g. Hoffmann *et al.* 2009); therefore, bark thickness has been found to be a better and more universal predictor of stem death (Hoffmann *et al.* 2009; Lawes *et al.* 2011a,b; Brando *et al.* 2012). Based on data from 56 species obtained from 15 fire events (Fig. 2a), a bark thickness of 5.9 mm is needed to ensure a 50% chance of surviving a low-intensity fire (flame length < 2 m). For high-intensity burns (flame length > 2 m), bark

thickness of 9.1 mm is required to reach this level of safety (Fig. 2a). For the sake of simplicity, and because savanna fires from natural ignitions tend to occur at times of year when fire intensity is typically low (Ramos-Neto & Pivello 2000), we will consider a stem to have reached the fire-resistance threshold if it has accumulated at least 5.9 mm of bark.

In the transition between savanna and forest, multiple factors contribute to the decline in flammability as tree cover increases. Compared to open habitats, the forest understory is characterised by the lack of C_4 grasses (Ratnam *et al.* 2011), as well as a cooler, more humid and less windy microclimate (Uhl & Kauffman 1990; Ray *et al.* 2005). Although all of these variables contribute to the low flammability of forest, Hoffmann *et al.* (2011) found the loss of grasses to cause greater reductions in fire intensity, flame length and rate of spread than did changes in microclimate. Grasses enhance flammability primarily by reducing fuel bulk density, and only a small amount of grass biomass is needed to have this effect (Hoffmann *et al.* 2011). Thus, we consider a savanna to have transitioned to forest if the canopy is sufficiently dense to eliminate the C_4 grasses typical of savanna, in agreement with definitions commonly used to distinguish these biomes (Ratnam *et al.* 2011). Based on data from savannas and forest in central Brazil (Hoffmann *et al.* 2005; Silva *et al.* 2008, 2010; Geiger *et al.* 2011), this threshold is reached when the leaf area index (LAI) of the overstorey reaches ~ 3.0 (Fig. 2b). Alternately, Archibald *et al.* (2009) found flammability to decline dramatically when tree cover exceeds 40%.

Although it is useful to assign fixed values to the fire-resistance and fire-suppression thresholds for heuristic reasons, this obscures the multitude of factors that influence flammability and topkill. For example grazing animals can render a savanna nonflammable by consuming fine fuels (Holdo *et al.* 2009; Midgley *et al.* 2010), and even closed-canopy forest can become flammable under extremely dry conditions (Ray *et al.* 2005). These quantitative shifts in the fire-suppression threshold are further complicated by the heterogeneity of tree cover that is characteristic of savanna systems. Even isolated trees can locally reduce flammability (Holdo 2005; Stevens & Beckage 2009), and mosaics of nonflammable vegetation patches may prevent fire spread even though the majority of a landscape is flammable (Collin *et al.* 2011). These spatial effects operating over multiple scales are important to the understanding of savanna-forest dynamics and deserve further study.

Any factor that influences ecosystem flammability has implications for fire intensity and, consequently, for topkill. These sources of variation in fire intensity can have large effects on tree dynamics through the strong effect of fire intensity on topkill (Fig. 2b; Ryan & Williams 2011). Although we focus here on the presence or absence of fire, variation in intensity should play a similar role, and its effects should ultimately be integrated into a framework for understanding savanna-forest dynamics.

INTERACTIONS BETWEEN THRESHOLDS AND RESOURCE AVAILABILITY

The two thresholds described above introduce considerable nonlinearity into savanna-forest dynamics because each acts as a tipping point, which, when crossed, results in a shift to a new regime characterised by substantial changes in structure and function (e.g. Groffman *et al.* 2006). The fire-resistance threshold and the fire-suppression threshold act in parallel manners because crossing either

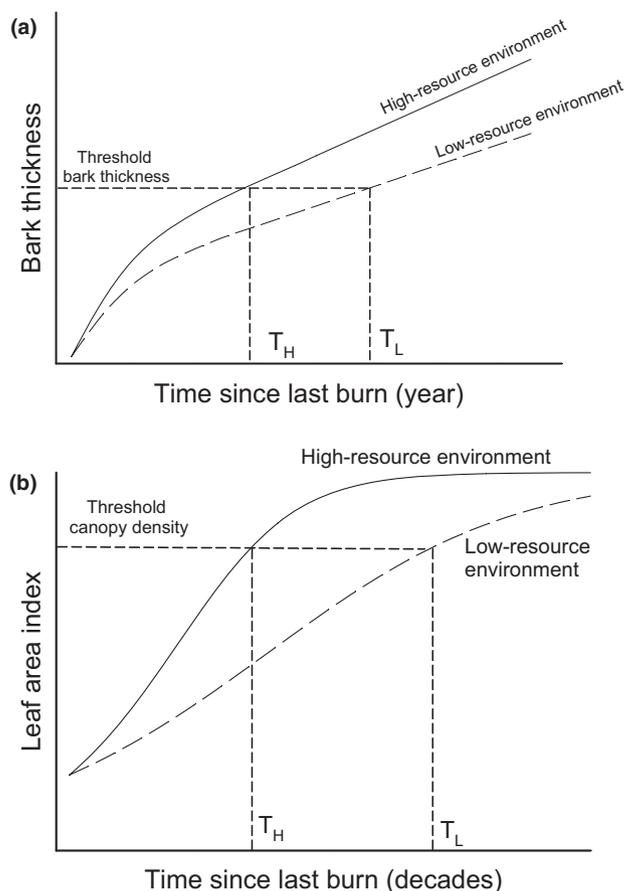


Figure 3 Graphical representation of the effect of resource availability on the time required to reach the (a) fire-resistance threshold of resprouting stems and the (b) fire-suppression threshold of the ecosystem. Resource availability determines the rate of stem growth and canopy closure respectively, hence the time required to reach either threshold is considerably shorter for the high-resource environment (T_H) than for the low-resource environment (T_L). Panel (b) was adapted from Lehmann *et al.* (2011).

threshold is largely dependent upon the length of time between successive fires. A stem, for example, will surpass the fire-resistance threshold and therefore escape the fire trap if the interval between fires is long enough to allow it to accumulate sufficient bark to avoid topkill. On the contrary, the fire-suppression threshold is surpassed if the interval between fires permits sufficient canopy closure to eliminate the continuous grass layer. Any factor that influences the time needed to reach either threshold can strongly influence tree dynamics.

Resource availability should influence this dynamic by affecting the time required to reach these thresholds (Fig. 3, Bond & Midgley 2000; Lehmann *et al.* 2011). In a low-resource, unproductive environment where plant growth is slow, a long fire-free interval is needed for a stem to accumulate sufficient bark to escape the fire trap (Fig. 3a) or for the ecosystem to accumulate sufficient tree leaf area to eliminate the highly flammable C_4 grasses (Fig. 3b). Thus, the occasional long fire-return interval will be of greater consequence than the average interval, as it is the extraordinarily long interval that can permit sufficient tree growth to allow either threshold to be surpassed. Stochasticity of the fire interval should therefore have a strong influence on vegetation dynamics (Higgins *et al.* 2000; Gardner 2006) by allowing for occasional fire-free periods that are much longer than the mean.

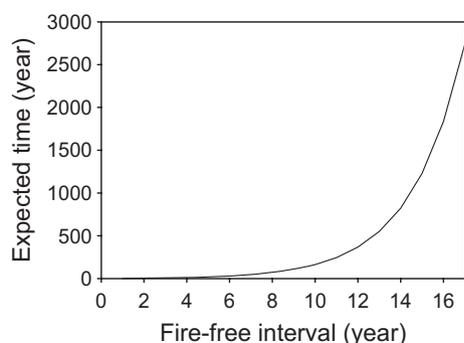


Figure 4 Expected total time required to observe a single fire-free interval of given length (T). The relationship assumes an annual probability of burning (p) of 0.33. The expected time is calculated as $(1-p^T)/(1-p) p^T$ (Johnson *et al.* 1992, p. 426). As shown, long fire-return intervals are expected to occur only rarely under fire regimes typical of savanna.

We lack information regarding the occurrence of extremely long fire intervals in savanna under typical fire regimes, but they are almost certainly rare. In mesic savanna, grass biomass approaches pre-burn levels quickly following fire (Govender *et al.* 2006); therefore, it is reasonable to approximate fire as a simple binomial process in which the probability of burning is independent of the time since last burn (McCarthy *et al.* 2001; Pueyo *et al.* 2011). Under this assumption, long fire-free intervals should be rare events in most mesic savannas worldwide (Fig. 4). For example if we assume that the annual probability of burning is 0.33, a reasonable value for many mesic savannas (Coutinho 1990; Barbosa & Fearnside 2005; Archibald *et al.* 2009; Russell-Smith *et al.* 2010), we would expect to observe a 9-year fire-free interval less than once per century (Fig. 4). A 15-year fire-free interval, however, should occur less than once per millennium (Fig. 4). These simple calculations ignore sources of variability, such as extreme events and climate fluctuations, that may become particularly important at long time scales. However, they illustrate that long intervals without fire are very unlikely events under fire regimes typical of mesic savannas, and therefore a modest increase in the rate of tree growth can dramatically increase the probability that a sapling reaches a fire-resistant size or that a site eventually becomes forest.

By governing the time needed for a state change, these ecological thresholds provide a mechanism for how resource availability interacts with fire to govern tree cover and the distribution of savanna and forest. This framework considers that the distribution of savanna and forest depends on the opposing processes of disturbance and succession. In unproductive environments, where tree growth is slow, the transition from savanna to forest will be a very rare occurrence. Any factor that increases the rates of tree growth and canopy closure should shorten the time necessary to reach these critical thresholds and will, therefore, tip the balance in favour of forest. In contrast, any factor that increases the frequency or intensity of fire should push the system towards savanna.

The interaction between tree growth rate and fire effects has been noted by others who have invoked similar arguments to predict tree encroachment under elevated CO_2 (Bond & Midgley 2000) and to explain the tendency for mesic savanna to be associated with nutrient-poor soils (Kellman 1984; Hoffmann *et al.* 2009; Lehmann *et al.* 2011) or seasonally dry climates (Lehmann *et al.* 2011). Similar arguments can be made for other factors that limit

tree success, such as seasonal flooding or shallow or sandy soils, all of which commonly support savanna but do not necessarily preclude forest when fire is absent. Therefore, it should not be surprising that savanna is broadly associated with multiple edaphic, climatic and hydrological stressors, although, locally, these factors often fail to explain the distribution of savanna and forest (Haridasan 1992; Hoffmann *et al.* 2009; Lehmann *et al.* 2011; Staver *et al.* 2011b). Weak or inconsistent correlations between vegetation and the physical environment suggest an important role of fire history and the action of rare events that may permit a local switch from one biome to another.

Although high resource availability can favour forest by accelerating tree growth, this effect should be offset somewhat by the effects on grass productivity and fine fuel mass. Across savanna regions as a whole, fire frequency is positively correlated with precipitation because of increased fuel accumulation in regions of high rainfall (Russell-Smith *et al.* 2007; Archibald *et al.* 2010). Within the high-rainfall mesic regions, further increases in precipitation have little effect on fire frequency (Archibald *et al.* 2010), but variation in soil nutrients should play a similar role. Here, nutrient loss by fires should reinforce the direct feedbacks between flammability and vegetation (Kellman 1984; Wood & Bowman 2012).

THE ROLE OF SPECIES TRAITS

Gignoux *et al.* (1997) called attention to the variation that exists among tree species in the time required to become fire resistant. This variation can arise because of differences in growth rate or in relative bark thickness (ratio of bark thickness to stem radius), either of which influences the rate of bark accumulation (Midgley *et al.* 2010) and can therefore form the basis for different fire-resistance strategies. As we show here, savanna species differ from forest species in both growth rate and relative bark thickness, with important consequences for their fire response.

Relative to savanna tree species, species typical of forest experience much greater rates of topkill during fire (Hoffmann *et al.* 2009), due primarily to their much thinner bark (Fig. 5a). Forest species are more susceptible to the fire trap because they must reach a larger size to accumulate sufficiently thick bark to provide adequate insulation against fire. This is offset somewhat by the tendency of forest species to grow more rapidly than savanna species, even when both are growing within the same savanna habitat (e.g. Rossatto *et al.* 2009).

As described in Appendix S1, we estimated the mean rates of bark accumulation for savanna and forest species, using field data on (1) the relationship between stem diameter and bark thickness (Fig. 5a), (2) the initial growth rates of resprouting stems following fire (Hoffmann *et al.* 2009) and (3) the annual diameter increment of established, unburned stems (Rossatto *et al.* 2009). Based on the projected increase in bark thickness, we estimate that a resprouting stem of a savanna species should typically require approximately 8 years to reach the fire-resistance threshold, whereas a forest species should require approximately 14 years (Fig. 6a). These differences are large, considering that under the stochastic fire regime described above, a fire-free interval of 8 years should be observed once every 74 years, whereas a fire-free interval of 14 years should be observed only once every 873 years (Fig. 4). Thus, under fire regimes typical of savanna, it is very improbable that a sapling of a forest tree will escape the fire trap and reach adult size. Individuals

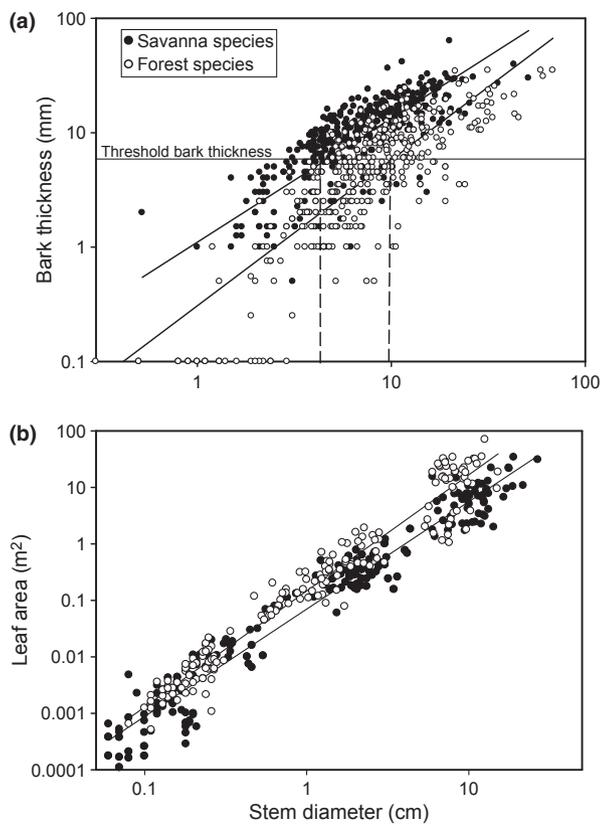


Figure 5 Comparison of allometric relationships of savanna and forest species. (a) Relationship between stem diameter and bark thickness compiled for 33 savanna species and 32 forest species (Hoffmann *et al.* 2003, 2009). The vertical lines indicate the diameters at which stems become resistant to low-intensity fires due to bark thickness of 5.9 mm. The fitted relationships are $Y = 1.105X^{1.083}$ (savanna) and $Y = 0.31X^{1.276}$ (forest). (b) Relationship between stem diameter and whole-plant leaf area. Each point represents one individual. Data were compiled from seedlings of 18 species (Hoffmann & Franco 2003), saplings of 30 species (Lau 2009) and adults of 20 species (Gotsch *et al.* 2010). The fitted relationships are $Y = 0.070X^{1.901}$ (savanna) and $Y = 0.147X^{2.053}$ (forest).

originating from seed would require even longer times than this, because initially seedlings grow more slowly than resprouts (Hoffmann 1998).

We based the above estimates on mean growth rates and bark thickness obtained from a large number of individuals and species. However, both quantities vary considerably within each species type. For those species with sufficient data, savanna species require from 3 to 24 years (median = 15) to accumulate 5.9 mm of bark, whereas forest species require from 16 to > 50 years (median = 31). Although these numbers suggest that even some savanna tree species are unlikely to escape the fire trap under frequent burning, they fail to account for variation in growth rate within species. In South African savannas, Wakeling *et al.* (2011) found that within species, the 5% of saplings with the highest growth rates can reach a fire-resistant size in half the time required for an individual growing at the mean growth rate. These fastest growing individuals could have substantial effects on vegetation structure, particularly where sapling densities are high (Wakeling *et al.* 2011). This effect is expected for both savanna and forest species, and should not influence their relative susceptibility to the fire trap.

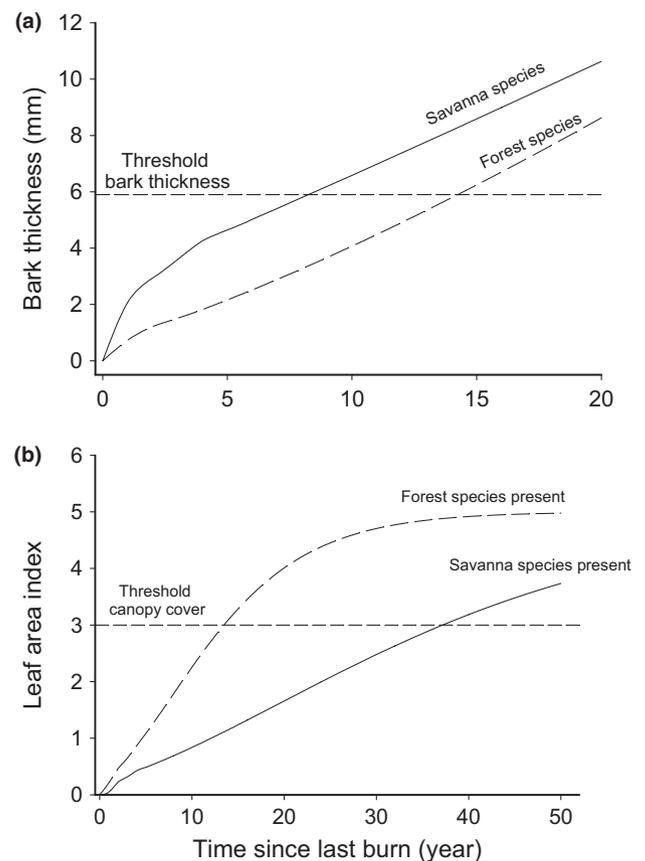


Figure 6 Estimates of times required for savanna and forest species to reach the critical thresholds during fire suppression. (a) Increases in bark thickness, based on projections of stem growth (Appendix S1), combined with the relationship between stem diameter and bark thickness (Fig. 5). Despite the more rapid growth of forest species, savanna species accumulate bark thickness more rapidly, thereby requiring less time to become fire resistant. (b) Projections of canopy density for stands composed entirely of either forest species or savanna species. Simple density-dependent effects were used to impose a maximum leaf area index of 5.0. Initial conditions were set to consist of stands of resprouting saplings at a density of 0.8 stems m^{-2} . See Appendices for more details.

Although savanna tree species are better able to reach the fire-resistance threshold in the interval between fires, the opposite is true for the fire-suppression threshold. Forest trees tend to have higher leaf area than savanna trees of similar size (Fig. 5b), which is manifested as both broader and denser crowns (Hoffmann *et al.* 2005; Rossatto *et al.* 2009; Gotsch *et al.* 2010). Therefore, where forest species are present, canopy closure should be more rapid than where only savanna species are present. Using a simple model of density dependence (Appendix S2), we estimate that a stand comprised of resprouts of forest species should require 14 years to reach a LAI of 3.0, compared to 37 years for a stand containing resprouts of only savanna species (Fig. 6b).

In our projections, we conservatively assumed that growth of savanna and forest species responds similarly to increasing canopy cover. If this assumption is incorrect, the role of forest species in the transition to a nonflammable state should be even greater than suggested by our projections. In fact, stands comprised solely of savanna species may be incapable of forming a canopy that is sufficiently dense to exclude savanna grasses entirely (Hoffmann *et al.*

2005; Ratnam *et al.* 2011) due to the strong shade intolerance and open crowns typical of savanna species. Published descriptions of the succession of fire-suppressed savanna indicate that the transition to forest is universally associated with the ingression of forest tree species (Bowman & Fensham 1991; San José & Fariñas 1991; Swaine *et al.* 1992; Russell-Smith 2004; Hennenberg *et al.* 2005; Pinheiro & Monteiro 2006; Geiger *et al.* 2011), although it is difficult to ascertain whether succession to forest is absolutely dependent upon the presence of these species. Regardless of whether it is possible to generate a forest physiognomy without the presence of forest species, they are generally present during this process and so their distinctly denser canopies and faster growth allow the canopy to close more quickly. In fact, under prolonged fire suppression, the recruitment of forest tree species can exceed that of savanna species (San José & Fariñas 1991; Russell-Smith 2004; Geiger *et al.* 2011), perhaps because of greater ability of many forest species to tolerate the partial shade provided by the increasingly dense canopy (Geiger *et al.* 2011), combined with more rapid growth.

The differences in the ecology of savanna and forest trees suggest an underlying tradeoff between fire tolerance and competitive ability. Adaptations to the savanna environment, such as large investment in carbohydrate reserves (Hoffmann *et al.* 2004), root biomass (Hoffmann & Franco 2003) and bark (Fig. 5a), represent large carbon costs which likely contribute to the slow growth of savanna species and their apparent inability to recruit in densely shaded environments. Neither of these characteristics, by itself, would necessarily prevent savanna trees from persisting in tropical forest, which supports both slow-growing climax species and shade-intolerant pioneers. However, the combination of slow growth and shade intolerance does not appear to be a viable strategy in forest, where high-light environments are short lived.

PERSISTENCE AND SEEDLING ESTABLISHMENT

In our calculations above, we did not consider the role of seedling establishment, but instead have assumed that all plants begin the fire-free interval as resprouts. For mesic savanna species, this assumption appears reasonable, since sapling densities are typically many times greater than those of adult trees (Prior *et al.* 2010; Durigan *et al.* 2002; Higgins *et al.* 2007; Geiger *et al.* 2011), suggesting that canopy cover is not limited primarily by seedling establishment. Resprouts tend to be much larger than seedlings and have greater initial growth rates; therefore, wherever they are present, they should dominate tree dynamics. Wherever a sufficient sapling bank is not present, however, tree dynamics will be strongly dependent on seedling establishment.

This is particularly relevant for forest species. In our experience, saplings of forest species are scarce in regularly burned savanna, although the reason has not been sufficiently studied. Physical or edaphic factors may impose some limitations on establishment of forest tree species (Bowman 1993; Hoffmann *et al.* 2004), but large increases in recruitment following fire suppression (San José & Fariñas 1991; Geiger *et al.* 2011) point to fire as the dominant factor limiting their persistence. Seedlings of forest species seem particularly vulnerable to fire (Hoffmann 2000; Gignoux *et al.* 2009), but once well established, most of the forest trees that invade savanna are to be able to resprout vigorously, at least after a single fire (Fensham *et al.* 2003; Hoffmann *et al.* 2009). It remains unclear, however, whether forest species can generally resprout repeatedly

under frequent fire. We have not had the opportunity to observe the response of forest species to repeated savanna fires, but results from the Australian savannas indicate that survival of forest species is greatly reduced by repeated burning (Fensham *et al.* 2003). Certainly more information is needed to understand the failure of forest species to maintain a persistent sapling bank in frequently burned savanna. It is similarly important to understand conditions under which even savanna species may fail to persist, as this may explain the existence of an entirely treeless state which also occurs over parts of the tropics (Hirota *et al.* 2011).

Regardless of the cause, the lack of a persistent sapling bank should increase the time interval required for forest species to reach the fire-resistance threshold. Growth of new seedlings will be delayed, relative to existing stems, thereby further constraining the ability of forest species to reach a fire-resistant size between fires. We have therefore probably underestimated the difference in the times required for forest and savanna species to escape the fire trap. On the contrary, we may have overestimated the extent to which forest species can accelerate the rate of canopy closure; if forest saplings are not present prior to fire suppression, additional time will be required for them to establish and grow to sufficient size to influence vegetation structure.

IMPLICATIONS FOR VEGETATION MODELLING

As the understanding of savanna-forest dynamics grows, there will be opportunities to improve the representation of tropical biomes in vegetation models. Many dynamic vegetation models already incorporate fire (e.g. Thonicke *et al.* 2001; Arora & Boer 2005; Scheiter & Higgins 2009), and we expect continued improvements in the ability to simulate both the occurrence and impacts of fire. Particular attention should be given to the representation of the fire-resistance and fire-suppression thresholds because of their importance for vegetation dynamics. Several demography-based models of savanna tree dynamics have simulated the topkill process and, therefore, the fire-resistance threshold (Hoffmann 1999; Higgins *et al.* 2000; Gardner 2006; Holdo *et al.* 2009; Loudermilk *et al.* 2011; Ryan & Williams 2011). A greater challenge exists for larger-scale models that typically do not simulate the dynamics of individual stems. Hanan *et al.* (2008) showed that juvenile and adult stages could be simply incorporated to represent the fire trap and thereby avoid biases in simulations of tree biomass. In this approach, which has been used by others (Higgins *et al.* 2007; Staver *et al.* 2011a), the transition from saplings to adults is governed by a fixed probability that is independent of the time that the plant has remained in the sapling class. This approach, therefore, does not impose a wait time that is inherent in the transition from sapling to adult, but it remains to be seen whether this has a substantive effect on simulations of tree dynamics.

With some recent exceptions (Beckage *et al.* 2009; Scheiter & Higgins 2009), few models have explicitly represented separate forest and savanna tree functional types. Representing both of these functional types should substantially improve the realism of modelling tropical biomes, considering the unique role that each plays in vegetation-fire feedbacks and in vegetation dynamics more generally. For biophysical land surface models, the inherent differences in growth rate, stature and crown density of savanna and forest species will have implications for exchanges of energy, water vapour and carbon with the atmosphere.

CONCLUSIONS

The two thresholds reviewed here play key roles in governing the dynamics of savanna and forest throughout the seasonally dry tropics. Specifically, they provide mechanisms by which fire interacts with climate, soil resources and atmospheric CO₂ concentrations to determine the distribution of savanna and forest. These factors, by influencing rates of tree growth, determine the amount of time needed to reach each threshold and, therefore, govern the switch from a state maintained by fire to a state that is relatively uninfluenced by fire. The transition from one state to the other depends on infrequent events; the transition from sapling to adult or from savanna to forest requires unusually long fire-free intervals, whereas the reverse transitions are favoured under prolonged drought when savanna fires are sufficiently intense to cause substantial topkill of adult trees and when undisturbed forest becomes flammable. Thus, the balance between forest advance and retreat can be upset by human-induced changes in the frequency of these events.

By explicitly considering the role of tree growth and canopy closure for savanna–forest dynamics, we must recognise the importance of any factor that limits tree productivity. Locally, tree success may be limited by seasonal soil flooding, shallow soils, low nutrient availability, rocky or sandy soils or climate. As a result, savanna occurs over a vast range of conditions that have little in common except for their inability to support rapid tree growth.

Savanna and forest species play distinct roles in the fire-resistance and fire-suppression thresholds due to differences in growth rates, bark thickness, shade tolerance and crown density. Specifically, due to thin bark, forest tree species are largely unable to reach the fire-resistance threshold under fire regimes typical of savanna. Savanna trees, however, have limited capacity to transform ecosystems into a nonflammable forest state, due to their open crowns, low growth rates and shade intolerance. These differences reinforce the fire feedbacks that result in alternate states as well as the largely non-overlapping distributions of savanna and forest species across savanna–forest boundaries.

Identifying the transition points for the fire-resistance and fire-suppression thresholds provides us with reference points for interpreting the drivers of vegetation dynamics. We have found bark thickness and LAI to be robust, unambiguous and easily measured indicators of these transitions, but further research is needed to refine the ability to identify precisely the transition points for savanna–forest systems worldwide. More importantly, however, we need an improved understanding of multiple environmental controls over rates of tree growth and canopy closure, as these have profound influence on the balance between forest advance and retreat. Without this information, we will have a limited capacity to project the future distributions of savanna and forest biomes under changing climate, CO₂ concentrations and disturbance regimes.

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AUTHORSHIP

WAH, MH and ACF conceived and designed the studies and synthesis. WAH, ELG, SGG, DRR, LCRS and OLL collected the data. WAH prepared the first draft of the article and all other authors provided input on subsequent versions.

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