How do small savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark thickness

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Abstract. To recruit to reproductive size in fire-prone savannas, juvenile trees must avoid stem mortality (topkill) by fire. Theory suggests they either grow tall, raising apical buds above the flames, or wide, buffering the stem from fire. However, growing tall or wide is of no advantage without stem protection from fire. In Litchfield National Park, northern Australia, we explored the importance of bark thickness to stem survival following fire in a eucalypt-dominated tropical savanna. We measured bark thickness, prefire height, stem diameter and resprouting responses of small stems under conditions of low to moderate fire intensity. Fire induced mortality was low (<10%), topkill was uncommon (<11% of 5 m to 37% of 1 m tall stems) and epicormic resprouting was common. Topkill was correlated only with absolute bark thickness and not with stem height or width. Thus, observed height and diameter growth responses of small stems are likely different pathways to achieving bark thick enough to protect buds and the vascular cambium. Juvenile height was traded off against the cost of thick bark, so that wide stems were short with thicker bark for a given height. The fire resilience threshold for bark thickness differed between tall (4–5 mm) and wide individuals (8–9 mm), yet tall stems had lower $P_{Topkill}$ for a given bark thickness. Trends in $P_{Topkill}$ reflected eucalypt versus non-eucalypt differences. Eucalypts had thinner bark than non-eucalypts but lower $P_{Topkill}$. With deeply embedded epicormic buds eucalypts do not need thick bark to protect buds and can allocate resources to height growth. Our data suggest the only 'strategy' for avoiding topkill in fire-prone systems is to optimise bark thickness to maximise stem bud and cambium protection. Thus, escape height is the height at which bark protects the stem and a wide stem per se is insufficient protection from fire without thick bark. Consequently, absolute bark thickness is crucial to explanations of species differences in topkill, resprouting response and tree community composition in fire-prone savannas. Bark thickness and the associated mechanism of bud protection offer a proximate explanation for the dominance of eucalypts in Australian tropical savannas.

Key words: diameter-response; epicormic sprouting; eucalypts; height-response; stem death; topkill; tropical savanna.

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INTRODUCTION

Fire is an important driver of tree dynamics in savannas worldwide because it can limit seedling recruitment and prevent the transition of juvenile trees to the canopy (Prior et al. 2006, Bond 2008,

Midgley et al. 2010, Murphy et al. 2010). Juvenile trees most strongly experience the impact of fire because their entire above ground biomass is within the flame zone. Although mortality is low, juveniles may lose all above ground height and resprout from their base (topkill; sensu Bond and Van Wilgen 1996) or if they lose their canopy, they may resprout from the surviving stem. Repeated topkill of small trees prevents recruitment into adult size classes and may 'trap' individual stems in the flame zone (sensu Midgley and Bond 2001). In fact, the suppressive effect of fire on small savanna trees is such that topkill has become an accepted driver of savanna dynamics worldwide (Higgins et al. 2000, Hoffmann and Solbrig 2003, Balfour and Midgley 2006, Higgins et al. 2007, Hoffmann et al. 2009, Lehmann et al. 2009). Clearly, trees that are resilient to the damaging effects of fire and can avoid topkill will be advantaged in fire-prone savannas.

Resprouting is an effective response to fire as it shortens individual recovery time. After disturbance, resprouting from vegetative tissue buffers the infrequent recruitment of seedlings and facilitates persistence and population maintenance in disturbance-prone environments (Bond and Midgley 2001). Epicormic resprouting (sprouts arising from epicormic buds beneath or in the bark of a stem or branch on a plant) is particularly important because it restores photosynthetic capacity more rapidly than basal resprouting in topkilled individuals. Thus, epicormic resprouting is inextricably linked to those plant functional traits that protect buds, conferring resilience to fire and topkill, and make escape from the fire-trap possible. In particular, the role of bark thickness in protecting trees and epicormic buds from fire has been underappreciated (Burrows 2002, Burrows et al. 2008). Here we examine the role of bark thickness in enabling savanna trees to escape the fire-trap.

Currently, two hypotheses exist for how juveniles of many savanna trees develop resilience to fire and may escape topkill: (1) height-response, growing quickly and tall (escape height), which allows apical buds to escape being scorched (Higgins et al. 2000, Bond 2008, Burrows et al. 2008); and (2) diameter-response, growing a thicker stem (escape diameter) and thus being buffered against the heat of the fire

(Uhl and Kauffman 1990, Balfour and Midgley 2006), which can be achieved by having thick bark (bark thickness) and/or other bud protection such as deeply embedded meristems (Gill and Ashton 1968, Vines 1968, Gill 1995, Gignoux et al. 1997, Burrows 2002, Hoffmann et al. 2009, Midgley et al. 2010, Waters et al. 2010). Because there is a positive nonlinear relationship between bark thickness and tree diameter and height (Pinard and Huffman 1997, Werner and Murphy 2001, Hoffmann et al. 2003, Nefabas and Gambiza 2007, Williams et al. 2007), a relatively thin barked species but faster growing individual may match the fire-proofing of thicker-barked species, within a given inter-fire period, by relatively faster rates of height growth. Although bark thickness is implicated in fire resilience, it has received much less attention as an explanation for the general fire resilience of savanna trees than either the escape diameter or escape height hypotheses (cf. Gignoux et al. 1997, Pinard and Huffman 1997, Nefabas and Gambiza 2007, but see Hoffmann et al. 2009).

In seeking generalisations about the role and function of bark thickness in fire resilience and fire ecology, we examined tree responses to fire in a typical fire-prone tropical savanna in north Australia. We address the following questions: (1) how common is topkill (i.e., stem mortality or basal resprouting) among saplings in the flame zone of a typical eucalypt-dominated fire-prone savanna; (2) does plant height or stem thickness per se best predict the likelihood of topkill; (3) how do the dominant species and species groups (eucalypts vs. non-eucalypts) in this fire-prone savanna differ in terms of their height, width and bark thickness, and thus in their fire resilience; and (4) what is the role of bark thickness in protecting stems and in recovery from fire? We used inter-specific comparisons of post-fire responses to determine whether height, bark thickness or stem diameter is the most important predictor of post-fire response.

STUDY AREA

The data derive from Litchfield National Park (LNP; 1,464 km^2) in northern Australia (Fig. 1). The vegetation is dominated by eucalypt open forests and woodlands, with a grassy understorey, referred to hereafter as tropical savanna.
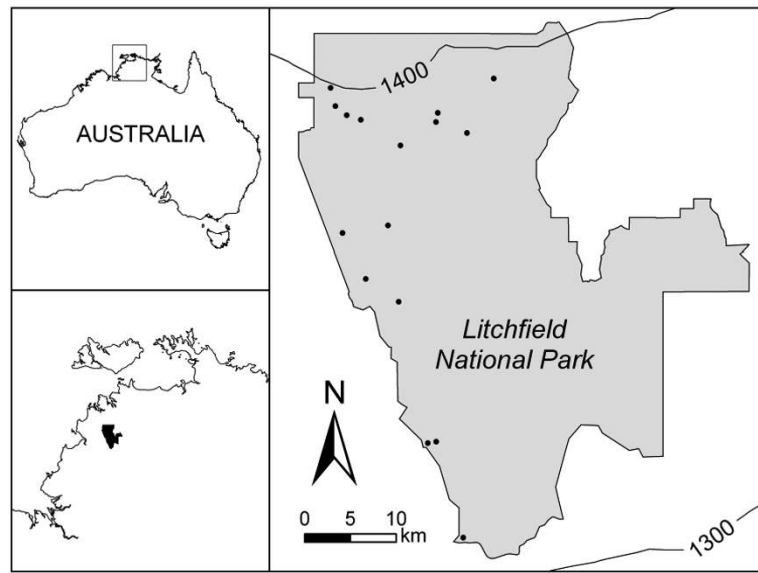
Fig. 1. Location of the 16 vegetation monitoring plots in mesic tropical savanna throughout Litchfield National Park in northern Australia. Contour lines represent mean annual rainfall (mm).

The climate is typical of monsoonal northern Australia, with high, extremely seasonal rainfall, ranging from ~1300 mm annually in the south to ~1400 mm in the north (Fig. 1), with 90% typically occurring during the summer wet season (*c*. December–April). This climate is particularly conducive to high fire frequencies: the wet season is highly productive with abundant grass growth, while the 7 month dry season (*c*. May–November) strongly promotes grass curing and flammability. In recent years, on average 66% of LNP was burnt per annum (Russell-Smith et al. 2009) by natural, lightening strike fires.

Between March 1994 and August 1996, 41 vegetation monitoring plots (20 m × 40 m) were established in LNP. Three vegetation inventories at approximately 5 year intervals have been carried out since. In June 2009 we surveyed all stems in 16 of the plots that were located in tropical savanna, that had been burned at least in the previous dry season or more recently, and had been burned in at least five of the previous twelve years. Monitoring plot data indicate that 86% of fires in LNP are of low (<2 m scorch height) or moderate (sub-canopy scorch) severity, with an average fire return interval ~1.5 years (Bushfires NT, unpublished data). Fire severity in the plots we surveyed was of low to moderate intensity.

METHODS

Measuring response to fire: height and diameter, resprouting and bark thickness

To control for differences in fire history, in each plot we compared bark thickness trends for individuals from co-occurring species with apparent competing responses (i.e., height- vs. diameter-response) for escaping the effect of fire. Furthermore, because height, bark thickness and stem diameter are correlated it is difficult to separate out the influence of height versus diameter and bark thickness within a species. To avoid this we compared mixed species pairs in a plot. Typically this included the dominant species in a plot, normally a eucalypt (*Eucalyptus* and *Corymbia* spp.), compared with a non-eucalypt species. At the juvenile stage, eucalypts typically have relatively tall stems for a given stem diameter and represent the height-response strategy, whereas non-eucalypts tend to have relatively short stems for a given stem diameter and generally represent the diameter-response strategy.

Individuals were characterised as 'tall' (height-response individuals) or as 'wide' (diameter-response individuals). If the ratio of stem diameter (mm) to pre-fire height (cm) was <0.2 a stem was regarded as tall, while a ratio >0.4

was indicative of a wide stem. Tall stems were operationally distinguished from wide stems by narrow stem diameters (at 0.5 m height) for their height (usually >100 cm tall), while wide or diameter-response individuals had a wide stem for their height (usually <75 cm tall). Tall individuals tended to be eucalypts and wide individuals were mostly non-eucalypts.

For each individual we also measured pre-fire height (where a burnt stem was still standing), post-fire height (height of highest buds and sprouts on the stem; equals zero for a topkilled stem), stem diameter at 50 cm above the ground for small stems (<10 cm diameter at 1.3 m), stem diameter at 1.3 m (diameter at breast height; DBH), and three categories of resprouting response to fire: basal resprouting (at base and up to 5 cm height on stem; often denoting a topkilled stem, but not always); epicormic sprouts on the main stem; and canopy sprouts (canopy is >90% of pre-fire height). Dead individuals were included in the analyses and scored as topkilled. Lastly, we took three measures of bark thickness at 50 cm height on the stem.

Bark thickness was measured using a standard thickness gauge (Haglöf, Barktax, Sweden) or where bark was not penetrable using the gauge, we used a needle punch (diam. = 2.5 mm). In both cases the gauge was inserted to the point of resistance by the sapwood. Bark thickness measured by this method includes the cambium in most instances. The distance from sap wood to bark surface was taken as the bark thickness. Where bark was corrugated we measured thickness from the highest point of the corrugation.

All sampling was conducted in mid-June 2009, about one month after early dry season fires, in plots that had been subjected to fire. Nineteen tree species were sampled from 1020 individuals. A subset of 398 juvenile stems from the nineteen species was examined in this study (Table 1).

Bark thickness allometry

In each plot we sampled (see metrics above) a minimum of 15 individuals from across the stem size range for each species representing either the height- or diameter-response. We compared the slope and intercepts of the relationship between bark thickness and tree height, and bark thickness and stem diameter for species representing

the two competing fire escape responses.

Data analyses

The probability of topkill and the relative importance of bark thickness, stem diameter and prefire height of individuals to stem survival and persistence, were analysed by logistic regression with topkill as the binary response variable. Differences in bark thickness between species adopting height- as opposed to diameter-responses to escape fire effects were analysed using randomised block ANOVA with species as the main treatment factor and data blocked by plot to effect plot-based species comparisons and to account for varying fire intensity among plots. All analyses were conducted using GenStat 12 Edition (GenStat 2009).

Results

How prevalent is topkill?

Topkill was uncommon (<15%) in tall stems (>4 m height) and common (~40%) in very short stems (<1 m height; Fig. 2A). Mortality was surprisingly low (Fig. 2A) and testament to the universal resprouting response among savanna trees. In most cases fire only caused a small reduction (~10–20%) of pre-fire height (Fig. 2B) and resprouting from the surviving stems (epicormic sprouts) or basal sprouts in the case of topkilled individuals, was common. A small number of mainly small (<2 m tall) individuals sprouted vigorously after the fire (during the approximately 6 weeks since the fire) from apical buds and were taller after than before the fire (Fig. 2B).

Why are small stems so fire resistant?

The importance of bark thickness to the fire resistance of individual trees (categorised as escape by either wide diameter or tall height) was confirmed by a logistic regression of the binary event of topkill against stem diameter, prefire height and bark thickness ($G^2 = 22.11$, $P < 0.001$). The likelihood of topkill was significantly related to absolute bark thickness only ($t_{slope} > -2.3$, $P < 0.02$; Wald statistic = 43.3, $P < 0.001$; Fig. 3). However, because bark thickness, prefire height and stem diameter were correlated ($r > 0.46$, $P < 0.001$) and this can affect the outcome of multivariate analyses, we examined the influence

Table 1. Summary of the sprouting and growth response to fires of low to moderate severity, bark thickness (BT) and bark morphology of the 19 species examined in this study. Note that all species listed here, except the reseeders, are capable of basal resprouting in response to intense fires.

| Family/Species | T/W | Mean BT (mm) | Diam. (mm) | Bark morphology | | Fire response of saplings |
				Saplings	Adults	
Anacardiaceae						
Buchanania obovata	W	8.3	36.5	Scaly	Cracked, corky	Basal and epicormic resprouting
Ceasalpiniaceae						
Erythrophleum chlorostachys	W	4.7	24.1	Fibrous, fissured	Corky, corrugated	Basal sprouts, occasional epicormic resprouts
Combretaceae						
Terminalia carpentariae	W	4.2	21.9	Smooth, soft	Smooth, spongy	Apical and epicormic sprouting
Terminalia latipes	W	10.2	75.6	Smooth	Smooth, finely fissured	Apical sprouting, basal sprouts in very small stems
Cupressaceae						
Callitris intratropica	T	3.2	25.5	Woody, furrowed	Woody, furrowed	Topkill; reseeder
Euphorbiaceae						
Petalostigma pubescens	T	4.5	22.0	Rough, woody, fissured	Rough, woody, fissured	Apical and epicormic sprouting
Myrtaceace						
Corymbia grandifolia	T	3.6	33.8	Scaly	Smooth	Epicormic resprouts
Corymbia polysciada	T	5.7	60.1	Scaly	Smooth	Epicormic resprouts
Corymbia ptychocarpa	T	5.4	28.4	Scaly	Smooth	Epicormic resprouts
Eucalyptus miniata	T	4.9	30.8	Scaly	Woolly mat over smooth bark	Basal and epicormic sprouting
Eucalyptus tetrodonta	T	4.1	23.8	Leathery	Leathery, stringy	Epicormic resprouting
Syzygium eucalyptoides subsp. *bleeseri*	W	3.8	28.7	Smooth	Cracked bark, smooth	Basal or apical sprouting
Lophostemon lactifluus	T	5.3	28.5	Scaly	Flaky, fibrous	Basal and epicormic sprouting
Melaleuca nervosa	T	4.0	17.3	Fibrous, flaky	Papery, fibrous, layered	Basal and epicormic sprouting
Melaleuca viridiflora	T	4.3	32.5	Fibrous, flaky	Papery, fibrous, layered	Basal and epicormic sprouting
Proteaceae						
Banksia dentata	W	4.6	21.9	Leathery	Leathery, furrowed	Topkilled or apical sprouts
Grevillea pteridifolia	T	2.7	14.9	Woody, rough	Woody, rough	Reseeder usually, but epicormic resprouting observed
Persoonia falcata	W	9.6	46.2	Leathery	Rough, flaky	Apical and epicormic sprouting
Rhamnaceae						
Alphitonia excelsa	W	5.2	35.4	Smooth	Smooth	Topkilled or apical sprouts

Note: T/W = Tall or Wide stem; Diam. is mean diameter at 0.5 m.

of each independent variable in turn using an information theoretic model selection approach (Table 2). The latter confirms the importance of bark thickness ($w_+ = 1$) relative to stem diameter ($w_+ = 0.29$) and prefire height ($w_+ = 0.27$).

Surprisingly, for a given bark thickness, topkill was significantly more likely for wide individuals than for tall individuals (Wald statistic = 42.3, $P < 0.01$; Fig. 3C). This unexpected result suggests that tall individuals (mainly eucalypt species) achieve lower rates of topkill in ways allied to, but not entirely explained by bark thickness. In general, the bark thickness required to ensure <20% likelihood of topkill appears to be approximately 4–5 mm (Fig. 3A, B). Further support for a minimum bark thickness is demonstrated by successful tall or height-response individuals who appear to achieve, and thereafter maintain, a constant bark thickness of about 4 mm, compared to wide or diameter-response individuals in which bark thickness (at 0.5 m height) increases with tree height (Fig. 4A). Thus, while 4–5 mm bark thickness is adequate to avoid topkill of tall individuals (Fig. 3C),
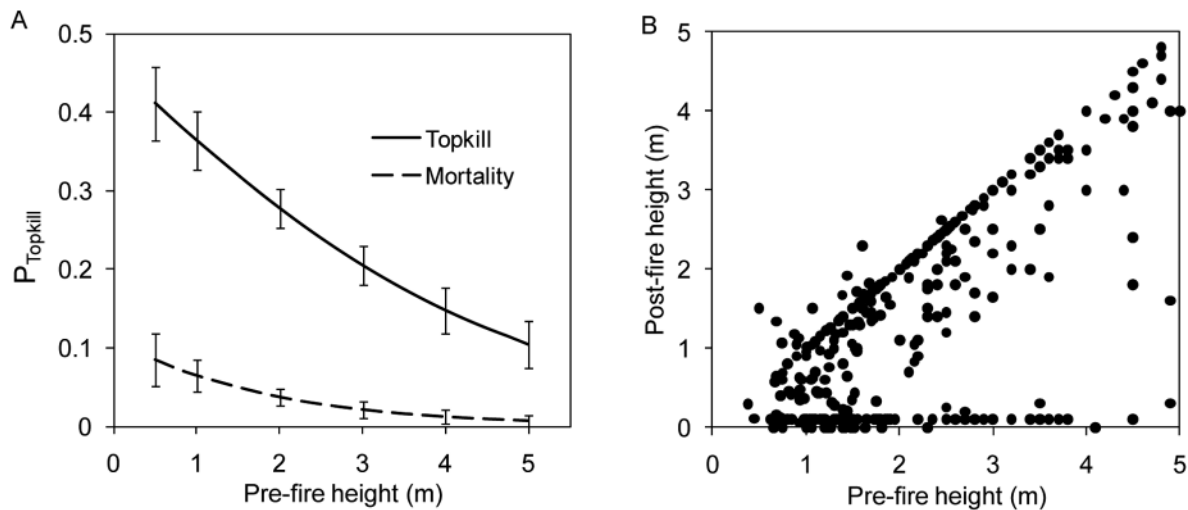
Fig. 2. Relationship between the probability (±1 SE) of (A) topkill or mortality, and (B) post- and pre-fire height, for small stems from 19 species. Stems with post-fire height of zero are dead individual stems. Mortality due to fire is rare and, although more stems are topkilled, most individuals either sprout from their base or, more frequently, from their stem, which means that fires cause mainly a loss of pre-fire dimensions.

wide-stemmed individuals either acquire thicker bark or require thicker bark (8–9 mm) to achieve similar low likelihoods of topkill (Fig. 3C).

In addition, topkill trends reflected eucalypt versus non-eucalypt differences (Fig. 3D). Eucalypts tended to be tall (escape height) for a given width, yet had lower likelihoods of topkill for thinner bark ($G^2 = 20.74$, $P = 0.001$; Wald statistic = 40.24, df = 2, $P = 0.001$). Again, this finding suggests that lower rates of topkill are not entirely explained by bark thickness and some other factor is involved.

Do individuals with thicker stems have thicker bark?

Diameter-response individuals with wider stems were much shorter than tall height-response individuals for a given bark thickness (Fig. 4A). However, without data on height growth rates we were not able to determine whether thicker bark is achieved at a cost to height growth, although this is likely. Bark thickness scaled as a power function of stem diameter at a faster rate for diameter-response individuals (slope = 0.516, $t = 71.5$, $P < 0.0001$; R^2 = 0.96) than height-response individuals (slope = 0.436, $t = 64.5$, $P < 0.0001$; R^2 = 0.96; Fig. 4B). Thus, wide individuals had thicker bark for both their stem diameter and height than tall individuals.

Bark thickness and 'escapers' vs. 'non-escapers'

Those individuals that did not escape the effects of fire were not confined to specific taxa, and the capacity for basal resprouting appears to be widely distributed (i.e., not constrained by phylogeny) among tree species in this fire-prone savanna. However, bark was thicker for non-eucalypt saplings (mean ± SE = 6.11 ± 0.15 mm) than eucalypt saplings (mean ± SE = 4.33 ± 0.19 mm; $F_{1, 366} = 51.5$, $P < 0.001$).

As predicted, bark was significantly thinner ($F_{3, 365} = 39.1$, $P < 0.001$) and prefire height lower ($F_{3, 373} = 16.1$, $P < 0.001$) in those individuals that lost proportionally more of their aboveground biomass or were topkilled (Fig. 5). Individuals that lost less than 25% of their prefire height were also vigorous epicormic sprouters. The proportion of the stem retained after fire was overwhelmingly due to bark thickness ($t_{366} = -8.4$, $P < 0.001$) as opposed to the prefire height of the stem ($t_{366} = -0.6$, $P = 0.56$).

Species trends in escape responses and bark thickness

Species trends by plot (i.e., controlled for fire history) broadly supported the two proposed responses by tree saplings for escaping the effects of fire: (1) have a thick stem with bark that is relatively thick for a given height—escape
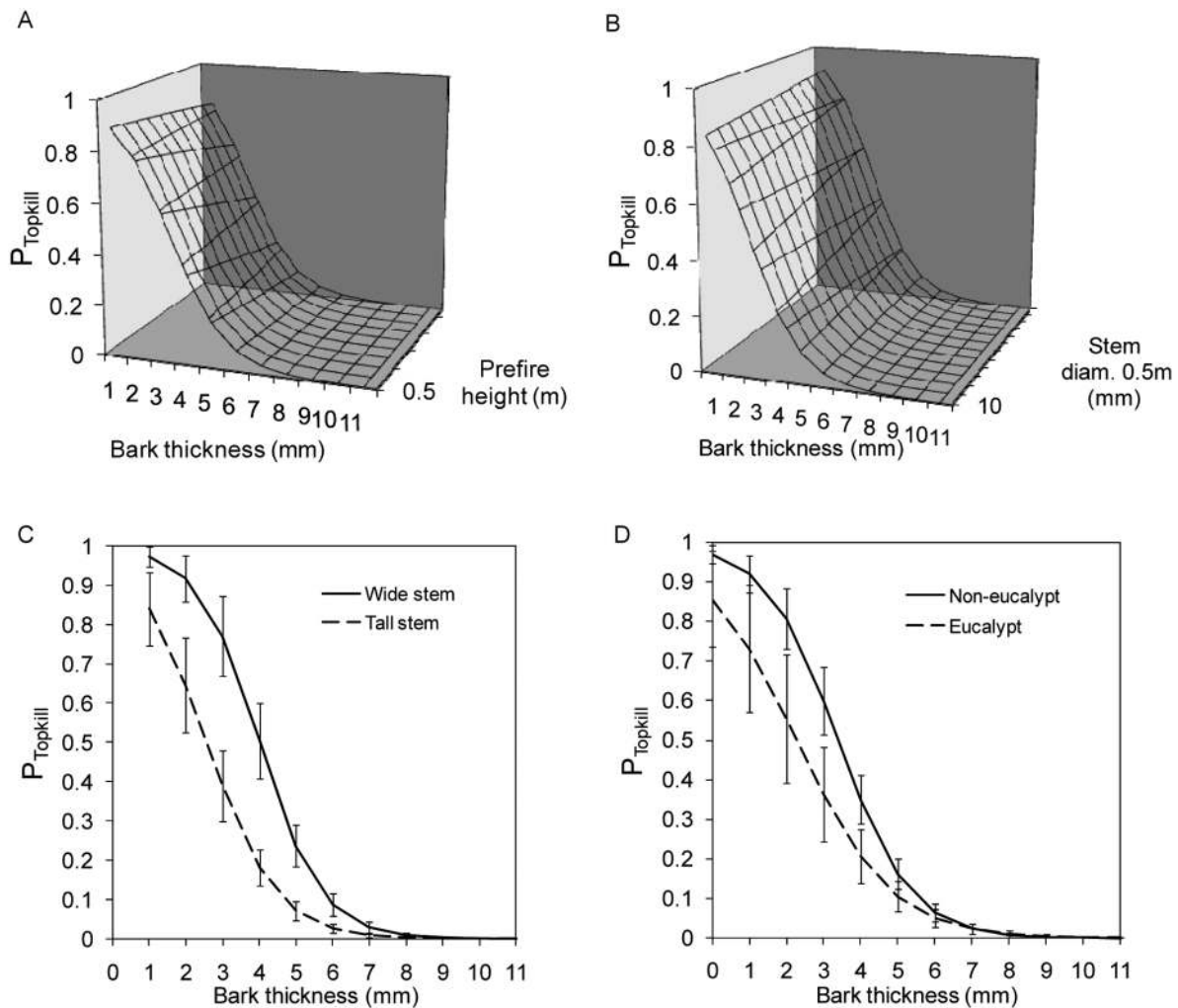
Fig. 3. Response surfaces derived from logistic regression of the probability of topkill ($P_{Topkill}$) in relation to bark thickness and (A) prefire height (with mean stem diameter at 0.5 m height = 30.9 mm), (B) stem diameter at 0.5 m height (with mean prefire height = 2.55 m). Surfaces demonstrate no influence of prefire height or stem diameter compared to bark thickness, on the likelihood that an individual will be topkilled. Shape of surfaces changed hardly at all for prefire height values ranging from 1 m to 6 m and stem diameter values ranging from 10 mm to 70 mm. Comparison of the relationship between bark thickness and $P_{Topkill}$ (± 1 SE) for individuals (C) in a priori categories of observed diameter or height (wide vs. tall stem), and (D) for eucalypt and non-eucalupt individuals.

diameter; or (2) have a tall stem with bark thickness in the flame zone sufficient to protect the stem from fire—escape height (Fig. 6). Height- (tall) and diameter- (wide) response individuals co-occurred in sample plots and bark thickness was significantly different between tall and wide individuals across the trends in prefire height for species in a plot ($F_{6, 351} = 9.39$, $P < 0.001$). The critical parameter for stem survival

and recovery in both strategies was the absolute thickness of the bark.

DISCUSSION

In this typical fire-prone tropical savanna, absolute bark thickness, as opposed to stem height or width, was the main reason for low rates of topkill after fire among stems in the

Table 2. Results of information theoretic model selection based on a logistic regression of the binary event of topkill against stem diameter, prefire height and bark thickness.

Model	AIC	ΔAIC	w_i	Explained deviance %	w_+
Bark thickness	297.2	0.0	0.52	32	1
Stem diameter at 0.5 m	357.5	60.3	0.00	18	0.29
Prefire height	400.3	103.2	0.00	8	0.27
Bark thickness + Stem diameter + Prefire height	300.9	3.7	0.08	32	

Note: AIC - Akaike's Information Criterion; w_i - the Akaike weight, representing the probability of a model being the 'best' in the candidate set; ΔAIC - is the difference between the model's AIC value and the minimum AIC of all models in the candidate set; Explained deviance - is the proportional reduction in residual deviance, relative to the null model; w_+ - is the probability of a given independent variable occurring in the best model and, therefore, reflects the weight of evidence of a relationship between the response (topkilled or not) and the given variable.

vulnerable sapling size-class. Epicormic resprouting from fire-damaged stems was common as a consequence of the bud-protective function of thick bark, ensuring that individuals quickly recovered their prefire stem height and biomass. The absolute bark thickness of tall or wide stems was the strongest determinant of interspecific differences in the likelihood of topkill. Although trees can persist through fire by either growing tall or wide (Archibald and Bond 2003, Balfour and Midgley 2006, Midgley et al. 2010), we argue that these apparent height- and diameter-responses are merely different allometric pathways

to achieving the thick bark needed to protect the stem and ensure rapid recovery from fire. Therefore, we suggest that there is in fact, only one 'strategy' for trees in fire-prone savannas, and that is to optimise bark thickness to maximise protection of the stem from fire and prevent topkill.

Bond (2008) argued that plant height is the most important predictor of topkill with a sharp decrease in topkill in plants that grow above a threshold size (escape-height), and furthermore, that bark properties should account for relatively small interspecific differences. In support of
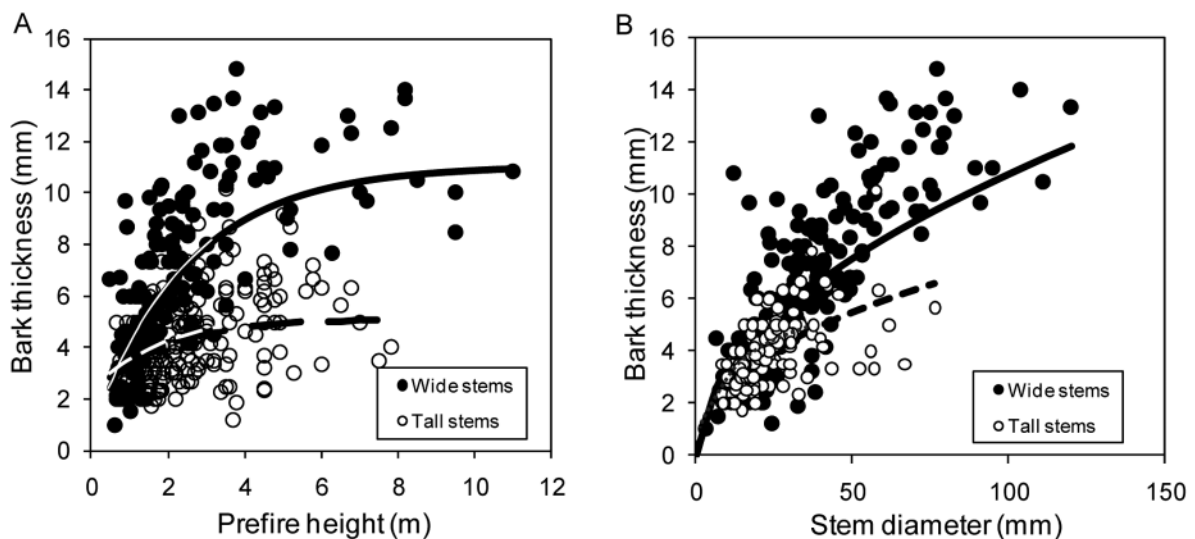

Fig. 4. (A) Relationship between bark thickness and prefire height of individuals that survived fire, showing that thicker bark is achieved by wide stems than tall stems. The threshold level of bark thickness required to resist the repeated effects of fire is approximately 4–5 mm and 10–11 mm for tall and wide individuals, respectively (i.e., the asymptote of bark thickness against prefire height). By 1 m tall, tall individuals approach the minimum threshold bark thickness of 4 mm. (B) Bark thickness scales as a power function of stem diameter for both tall and wide individuals, although at a more pronounced rate for wide individuals.
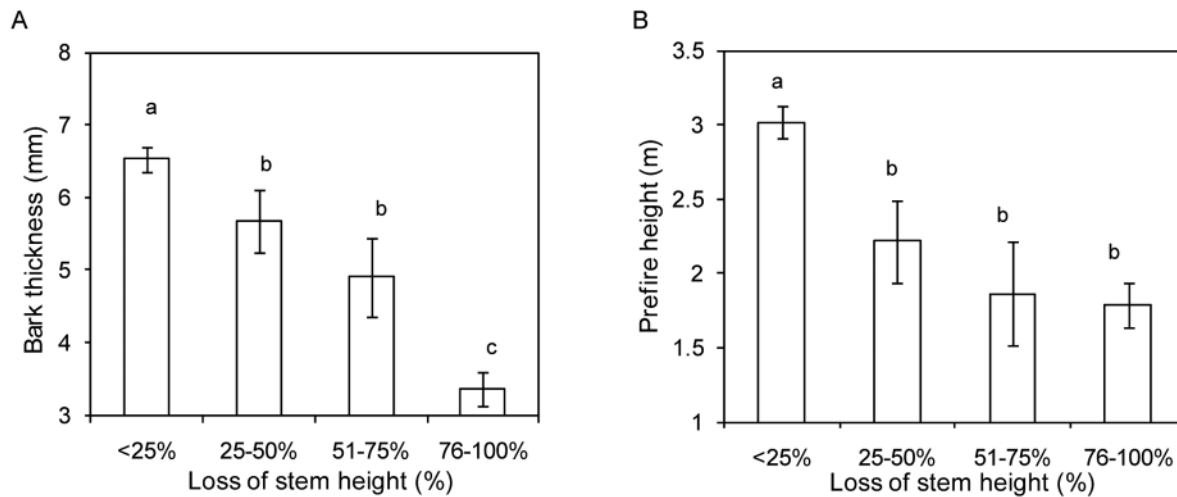
Fig. 5. Relationship between (A) bark thickness and (B) prefire height and the percent loss of stem height (proportional height at which the plant resprouted i.e., <25% indicates epicormic resprouting close to the prefire canopy height). Letters on the graph (a, b or c) indicate significant homogeneous groups based on Tukey's test.

Bond (2008), several African studies have noted that height growth rate is a sensitive parameter in models of tree population structure in frequently burnt savannas (e.g., Higgins et al. 2000, Higgins et al. 2007). However, many studies from both Africa and the Brazilian cerrado have also found that fire excludes faster growing forest species from savanna (Hoffmann and Solbrig 2003, Gignoux et al. 2009, Hoffmann et al. 2009), which is not expected if height growth rate is the key factor for survival in fire-prone savanna. Even though forest species grow more quickly than savanna species, in South America they are excluded from savanna (cerrado) by virtue of having thin bark (~20% of the relative bark thickness of savanna species) (Hoffmann and Franco 2003, Hoffmann et al. 2009). Furthermore, although fires in savanna (e.g., cerrado) are more intense and produce higher char-heights than forest fires, forest species suffer greater rates of topkill (Hoffmann et al. 2009). Rossatto et al. (2009) found that forest species grew (diameter growth) faster than did savanna species in cerrado, but their fire response (Hoffmann et al. 2009) suggests that forest species did not acquire thicker bark than savanna species. Similarly, although in Australia forest species grow faster than savanna species (Prior et al. 2004) they are excluded from savannas by fire impacts (Wilson and Bowman 1994, Russell-Smith et al. 2003,

Woinarski et al. 2004). More importantly in our study of a typical fire-prone Australian savanna, height-response or fast height growth per se did not explain the success of the eucalypts; by simply growing taller than the flame height, trees did not necessarily escape the effects of fire (cf. Balfour and Midgley 2006). We argue that it is not growth rates per se that predict where trees from different vegetation types occur in a fire-prone landscape. Other factors such as bark thickness and bark growth rates, the height of resprouting on the stem and the variability in the ability to resprout are critical in predicting which species persist in fire-prone areas (Gill 1995, Midgley et al. 2010).

In addition to recognising the importance of bark thickness to savanna tree dynamics under regimes of frequent fires (Hoffmann et al. 2009), there is a growing body of evidence that suggests that fire damage to the stem rather than the canopy crown is what kills trees (Gignoux et al. 1997, Pinard and Huffman 1997, Balfour and Midgley 2006, Nefabas and Gambiza 2007, Midgley et al. 2010). Balfour and Midgley (2006) demonstrated that among small stems in African savannas, the effects of fire on the xylem causes topkill. They emphasise the importance of stem traits (diameter growth rates, stem thickness, bark thickness) to the fire resilience of savanna trees. Thus, in general savanna species
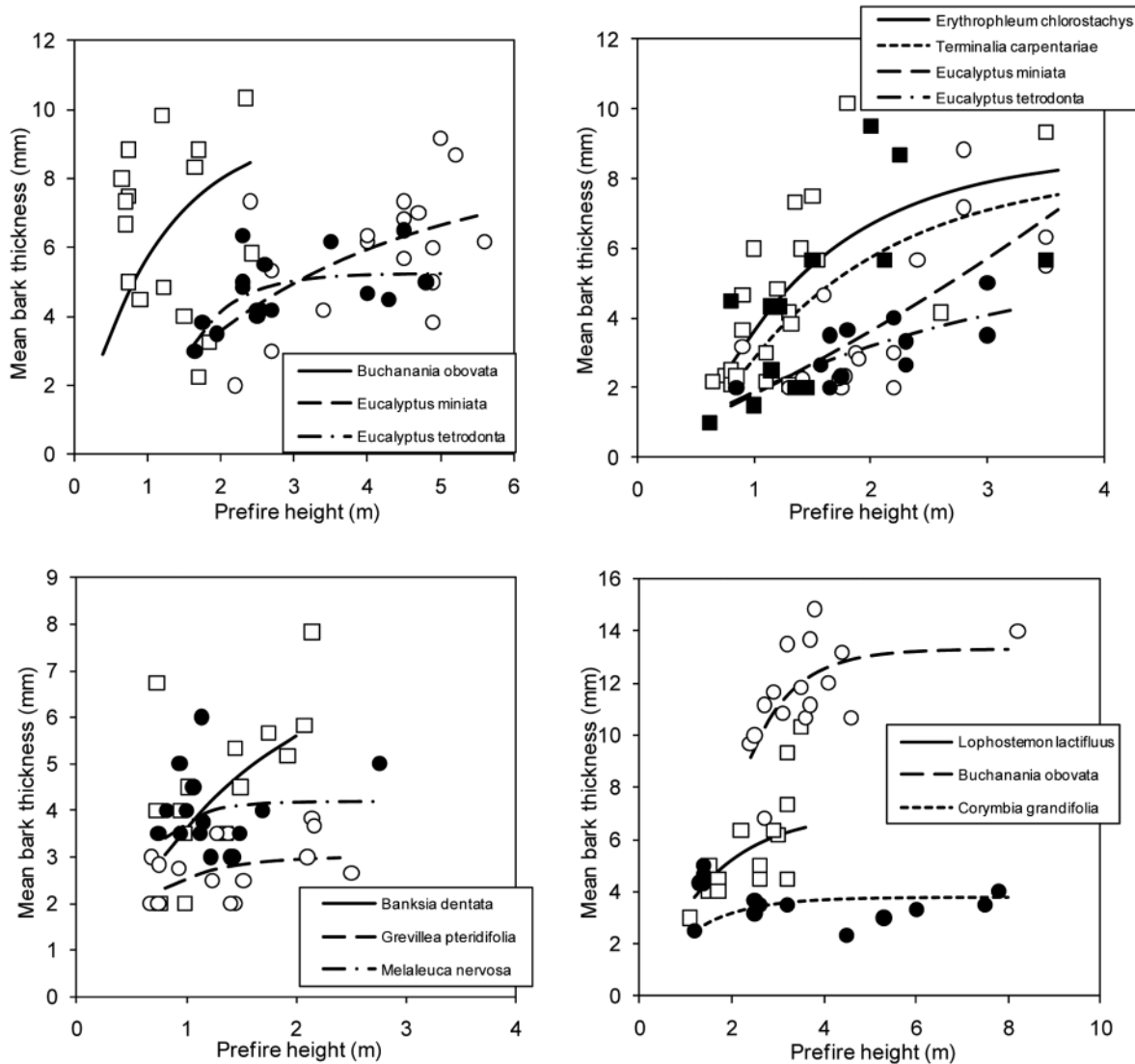
Fig. 6. Examples of competing responses for escaping the fire trap. The bark thickness versus prefire height trends are displayed for co-occurring species in a plot and thus site fire history is controlled for in these comparisons.

have evolved relatively thick bark (e.g., Hoffmann and Franco 2003, Hoffmann et al. 2009) in response to fire resulting in slower height growth rates than those of forest species because of their investment in thick bark (Midgley et al. 2010).

It is clear from our results that escape from and persistence through fire are only possible if savanna trees protect their stem from the effects of fire. They do this by having thick bark, which in turn can be achieved by either growing tall or by growing a thicker stem (Gill and Ashton 1968,

McArthur 1968, Gill 1995, Hegde et al. 1998, Barlow et al. 2003, Jones et al. 2006, Prior et al. 2010). We argue that if bark thickness is the most important determinant of fire resilience among trees, then the roles of diameter growth and especially height growth in escaping fire effects have been misinterpreted. For instance, by our argument, escape height is not the height at which the canopy is no longer damaged or scorched, but is the height at which bark is thick enough to protect the stem. By extension of this

argument, by growing tall trees not only escape the effect of the flames, they also ensure sufficient stem diameter and bark thickness for their stem to survive fire. Furthermore, radial or diameter growth per se is insufficient to protect the tree stem from the effects of fire without thick bark and rapid bark growth rates. The latter is clearly illustrated in the Brazilian cerrado by greater likelihoods of fire induced mortality of forest trees with thick stems but thin bark when compared to savanna trees with equally thick stems but thicker bark (Hoffmann et al. 2003). Again, the inescapable conclusion is that it is absolute bark thickness that is the most influential determinant of savanna trees ability to recover from and resist fire.

Our study raises the question of how the fast growing (height-response) individuals with thinner bark, mainly eucalypts (Prior et al. 2006, Prior et al. 2010), had higher rates of survival after fire than thicker-barked diameter-response individuals? Furthermore, an explanation for the co-occurrence of both height- and diameter-responses is required, especially considering that growing tall appears to have significant advantages over growing wide and thus would be expected to become the dominant response. Clearly, having thick bark is not the whole explanation for the success of tall individuals, but neither is their height above the flames of the fire, because fires seem to kill trees by damaging the stem, not the canopy (Balfour and Midgley 2006). There must be other aspects of bark or stem anatomy that facilitate the success of the eucalypts and the escape height strategy in general. Tropical savannas worldwide have been under selection pressure from fire for much of their evolutionary history (Bond and Van Wilgen 1996, Gill 1997, Williams et al. 1999, Bowman 2000). Accordingly, the dominant tree families in these savannas, for example the Myrtaceae (eucalypts) in Australia, display unique adaptations to fire that optimise the protective function of the bark and facilitate epicormic resprouting and comparatively rapid recovery from fires of low to moderate intensity (Burrows et al. 2010). It is now well known that in the eucalypts, epicormic buds are arranged along the stem on strands of meristematic appearance and these are deeply buried at the level of the vascular cambium, where they are protected by the maximum bark thickness (Burrows 2000, 2002). Deeply embedded epicormic strands means that eucalypts do not need thick bark to protect their buds. They can divert resources from bark growth to height growth, overtopping and out-competing non-eucalypts that employ diameter growth. Fast height growth rates achieve threshold bark thickness for stem and bud survival in the flame zone. Thus in Australian tropical savannas, where fires are of low to moderate intensity, eucalypts minimise loss of stem height to fire by resprouting from protected epicormic buds. They escape the fire-trap by optimising bark thickness through maximising height growth under disturbance.

Why don't all individuals grow tall in response to fire; why do individuals with wide stems but short stature also persist in fire-prone savannas? One answer may be that these growth responses reflect constraints on tree architecture under disturbance as a result of a trade-off at the sapling stage between vertical growth and radial growth (Ackerly and Donoghue 1998, Archibald and Bond 2003, Balfour and Midgley 2006). But, a simpler answer is that diameter-response individuals lack the epicormic strand structure of eucalypts (Burrows 2002) and thus have to protect their stem bud bank and the vascular cambium with thicker bark. By allocating resources to bark growth, diameter-response individuals constrain their height growth and tend to have shorter and wider stems than eucalypts. In Australia, species differences in epicormic bud anatomy and bark thickness provide a proximate explanation for the dominance of the eucalypts. Thus, bark thickness is the key to explaining not only interspecific differences in topkill, but also in resprouting response and tree community composition in fire-prone savannas.

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