

**PATTERNS AND MECHANISMS OF STEM MORTALITY IN *ACACIA*
NIGRESCENS INDUCED BY ELEPHANTS AND FIRE**

BY GLENN MONCRIEFF



Submitted in partial fulfillment of the degree of Bachelor of Science (Honours)

Botany Department
University of Cape Town

29 October 2007

Supervisors
A./Prof. Jeremy J. Midgely
Dr. Laurence M. Kruger

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Abstract

Increasing elephant populations have been implicated in the decline of woody vegetation throughout Africa. The problem is particularly relevant to the Kruger National Park in South Africa, where elephant populations have almost doubled in the last 10 years. One manner in which elephants utilize trees is by stripping their bark. The role of bark stripping in increasing stem vulnerability to fire and the mechanism through which fire damage is mediated were investigated by experimentally removing bark and burning *Acacia nigrescens* stems. Field surveys were conducted in order to investigate patterns of bark stripping in relation to mortality patterns of large trees occurring subsequent to natural fires. In the experimental study, an increasing probability of mortality was associated with increasing amount of bark removed when trees were burnt. However, when trees were stripped but not burnt, simulating damage to cambium and phloem, none died in the 4 month period over which the experiment ran. This was taken as evidence that fire-induced xylem damage causes stem mortality. However, fire did kill a greater proportion of the remaining stem cambium around the circumference when bark had been removed. The field surveys indicate that bark stripping by elephants is frequent on large stems (44%) and that larger trees are more heavily impacted. The only variable measured that explained mortality patterns well was the percent of bark removed around the stem circumference up to 3m ($p = 0.0076$). These results indicate that damage to xylem is important in determining post-fire survival and that bark stripping by elephants increases the vulnerability of stems to fire. This increased vulnerability is a result of both increased damage to cambium and damage to exposed xylem. The high proportion of trees stripped by elephants and the increase in vulnerability to mortality associated with bark stripping suggests that unless elephant population growth is curbed, large *Acacia nigrescens* trees will eventually be eliminated from this ecosystem.

Introduction

Acacias (*Acacia* spp.) and African elephants (*Loxodonta africana*) are both iconic symbols of African savannas, and are both important components of savanna ecosystems. However, their coexistence is unstable; elephants utilize trees in a number of ways that can lead to eventual mortality. The pattern of decreasing woody cover in the presence of increasing elephant densities has come to be known as ‘the elephant problem’ (Laws 1970, Caughley 1976). In recent decades the establishment of protected areas and the control of poaching have resulted in a steady increase in elephant numbers (Douglas-Hamilton 1987). However, this conservation success story has had repercussions for species other than the African elephant. Gradual conversion of wooded savanna to grassland by elephants has been observed throughout Africa (Beuchner and Dawkins 1961, Thomson 1975, Barnes 1983, McShane 1987, Ben-Shahar 1993, Eckhardt *et al* 2000). Habitat change is caused by the removal of large trees (Barnes 1983, Dublin 1995) and the prevention of seedling recruitment (Dublin 1995, Campbell *et al* 1996). This change has implications beyond the aesthetic. Modification of habitat structure caused by the reduction in density of large trees and an increase in the density of shrubby vegetation can alter ecosystem function and eliminate habitat-sensitive species (Joy Belsky 1994, Cumming *et al* 1997).

Elephants utilize trees in a variety of ways: they may remove foliage when foraging, break canopy branches, uprooted entire trees, break stems or strip bark. Certain types of utilization are concentrated on trees of a particular size. For example, Macgregor and O’Conner (2004) found uprooting and stem breakage to be concentrated on stems between 1m and 7m in riparian woodland, whilst the amount of bark removed increased with stem diameter. Gadd (2002) found stem breakage to be concentrated on stems ranging from 10-19.9cm in *Sclerocarya birrea*, with no stems larger than 40cm having been broken. She too found bark removal to accumulate on larger trees. Whilst it is clear how uprooting and stem breakage can result in the loss of large trees and the alteration of

habitat structure, the largest trees in the landscape ought to be impervious to these types of utilization. Other explanations need to be explored in order to explain the elephant induced loss of the largest trees from a landscape. One form of elephant utilization that is concentrated on the largest trees is bark stripping. Observations and experiments investigating patterns and mechanisms of mortality in large trees may help clarify the role of elephants in this interaction.

Despite their ability to drastically alter habitat structure and reduce woody biomass, it is likely that elephants are not the sole agents responsible for the loss of big trees. Another organism that strips bark from trees that has been implicated in the death of large trees is the crested porcupine (*Hystrix cristata*). In the case of porcupine damage, tree death results from an interaction between bark stripping by porcupines and fire, involving repeated burning of exposed tissue (Yeaton 1988). Thus, it is likely that the combined effects of elephant utilization, porcupine utilization and fire damage contribute to the of death large trees. Fire is known to be an important factor causing plant mortality or mortality of above ground tissues (topkill) in savanna trees (Trollope 1984, Bond and van Wilgen 1996, Gignoux *et al* 1997, Hoffman and Solbrig 2003). The coexistence of tree and grasses in savannas is dependent on its presence (Higgins *et al* 2000). Fire is said to prevent the encroachment of woody plants by limiting recruitment of trees into larger size classes. Stems caught within the flame height that have their canopy scorched will have to regrow above-ground tissues from the rootstock as canopy scorch kills terminal buds and ultimately causes the death of above ground biomass (Trollope 1984, Bond and van Wilgen 1996, Higgins *et al* 2000). Thus in this conceptual framework it is plant height that determines vulnerability to fire induced stem death. The death of large tress cannot be explained by this hypothesis. The canopies of large trees are well beyond flame height, the only structure being exposed to fire is the stem.

An alternative to plant height as the key determinant of fire survival is stem diameter. Fire-induced damage to stem tissues (cambium, phloem and xylem) may result in stem death (Hoffman and Solbrig 2003, Bova and Dickenson 2005, Balfour and Midgley 2006, Jones *et al* 2006). Trees that have their canopy beyond the reach of flames

may still be killed by fire if their bark is not thick enough to insulate vulnerable tissues from heat (Uhl and Kaufmann 1990, Pinard and Huffman 1997). The matter of which tissues are important and how much heat need be applied has received little attention until recently (Bova and Dickenson 2005, Balfour and Midgley 2006, Jones *et al* 2006). It has been assumed that heating of vascular cambium to temperatures greater than 60°C will result in stem mortality (Uhl and Kaufmann 1990, Pinard and Huffman 1997). This has been shown to be an oversimplification, and the process is now known to be rate-dependent, influence by both heating rate and the period of exposure (Dickinson and Johnson 2004, Jones *et al* 2006). Aside from cambium, another stem tissue shown to be damaged by fire is xylem (Balfour and Midgley 2006). Xylem damage has been shown to cause stem death, as well as crown damage shortly after fire (Hare 1965, Kavanaugh *et al* 1999, Pockman and Sperry 2000, Balfour and Midgley 2006). The burning of stem heartwood exposed by bark stripping to fire can cause a large tree to collapse due to the loss of mechanical support (Yeaton 1988).

The mode through which fire induced stem damage is mediated has implications for understanding and predicting elephant effects on large trees. The removal of bark from the stem reduces the amount of cambium around the circumference of the stem. This, in isolation, does not appear to be the cause of the death of large trees. MacGregor and O'Conner (2004) and Gadd (2002) showed that for bark stripping to cause stem death, trees had to be almost entirely ring-barked. Exposure of cambium adjacent to the area stripped of bark to heat or an increase in heat transfer through the stem may be involved in increasing the vulnerability of large trees to fire. Alternately, heating of exposed xylem may result in increased post-fire stress, ultimately increasing the probability of stem death. It may take several fires to weaken stem heartwood sufficiently to cause mechanical failure (Yeaton 1988). The invasion of exposed wood by wood-boring beetles has also been postulated as expediting stem death, as they created burrows and fissures in wood, perhaps ventilating fires and augmenting damage (Guy 1989).

Between the years 1966 to 1995, Kruger National Park authorities used culling to restrict the size of their elephant population to around 7500 individuals. However, public

pressure led to a moratorium being called on elephant culling in 1995. Since then the population has risen to ca. 14500 in 2007. This increase and the observation that the number of large trees has decreased throughout the park between the years 1940 and 1998 have caused concern regarding the impact of elephants on the woody vegetation (Eckhart *et al* 2000).

The knobthorn, *Acacia nigrescens* Oliv. is one of the most abundant and important tree species in the Kruger National Park (van Wyk and Fairall 1969). It is a medium to large deciduous tree, growing up to 30 meters, and forms an important part of the diet of many browsers (Schmidt *et al* 2002). It is broadly distributed throughout southern Africa, spanning a wide range of rainfall and soil fertility gradients and known to be heavily utilized by elephants where the two species co-occur.

In light of the increasing elephant population in Kruger National Park and the dearth of knowledge pertaining to fire impacts on adult acacias (Midgley and Bond 2001), further insight is needed in order to understand the interaction between elephants and fire and their impact at the scale of the individual tree. Landscape-scale surveys of the concentration and extent of utilization are required to determine its prevalence and to predict future trends and repercussions. The type of elephant utilization that is the subject of this study is bark stripping. Information is needed regarding the size based distribution of stripping and stripping intensity to determine which trees are most vulnerable. Since bark stripping only affects the stems of trees it is important to understand the relative importance of stem size, and hence bark thickness, in the post-fire survival of above ground biomass. One might expect that if stem diameter and bark thickness are important dimensions determining fire survival, then a relatively abrupt change in survival probability will be evident in the size class distribution of stems. This would be a result of the bark exceeding the critical thickness required in order to prevent the heating of stem tissues to lethal temperatures (Bova and Dickenson 2005). This relationship may however be altered by bark removal. The loss of trees following the introduction of elephants and their rising densities suggests that trees usually resistant to fire and other agents of mortality are rendered vulnerable by elephants somehow. One of the principle

functions of bark is to protect stem tissues from external damage. I hypothesize that the removal of bark by elephants increases the vulnerability of stems to fire induced damage. If this is true, then the removal of bark would result in stem death in trees that would otherwise have thick enough bark to resist fire. Multiple mechanisms through which this damage may be mediated have been mentioned. One of these is thermally induced cambium death. If bark removal increases the probability the remaining cambium being killed by fire, then it is possible that bark removal increases the probability of a stem having its entire circumference of cambium killed (ring-barking of the stem), and ultimately dying. However, if the total removal of bark in the absence of burning does not produce the same results as the combination of bark removal and burning then other mechanisms besides cambium damage need to be invoked. This is because the maximum damage a fire can possibly cause to stem cambium is to ring-bark it. These other mechanisms include damage to functioning xylem vessels, the burning of heartwood and structural weakening of trees in successive fires. The importance of fire damage to heartwood and the subsequent structural weakening of stems can be determined by relating patterns of mortality to the degree and extent of heartwood damage.

Through experimental manipulation of *Acacia nigrescens* stems, applying differing degrees of bark removal I aim to address the following questions:

- 1). How does the removal of bark influence the vulnerability of stems to fire induced mortality?
- 2). Which tissue damaged by fire ultimately determines stem survival?
- 3). How does bark removal affect fire damage to stem tissues?

Field surveys of *Acacia nigrescens* populations will be conducted in order to address these questions:

- 1). How well do the experimental results reflect actual patterns of mortality?
- 2). Which mechanism resulting in stem death best explains patterns of mortality in natural fires?
- 3). What is the extent of elephant utilization of *Acacia nigrescens* in the Kruger National Park?

- 4). What are the implications of these mortality patterns for future population demography of *Acacia nigrescens* in the Kruger National Park, taking into account the extent of elephants utilization, the effect of utilization on vulnerability to mortality and the mechanism responsible for stem mortality.

Methods

Study area

All experiments and fieldwork was conducted in and around the Kruger National Park, South Africa. The 1 898 458 ha park is located in the northeastern corner of South Africa, bordering Mozambique and Zimbabwe. Two distinct geological regions occur in then park, low nutrient, sandy soils derived from granite dominate in the west and high nutrient, clay soils derived from basalt dominate in the east. The mean annual rainfall for the entire park is roughly 500mm per annum, but considerable variability exists, with a general pattern of increasing variability from south to north. Experiments and field survey were done in and around the Skukuza and Tshokwane districts. The mean annual rainfall for Skukuza is 550mm. In Tshokwane the mean annual rainfall is 562mm. The landscape type in both study areas is Marula (*Sclerocarya birrea*)-Knobthorn (*Acacia nigrescens*) savanna (Gertenbach 1983)

Fire simulations

In order to control for fire intensity in all experiments and to produce a controlled, localized fire, a modified wick technique was used to burn stems (Hare 1965, Uhl and Kaufmann 1990). This method involves soaking a paraffin soaked wick around the stem of a tree and allowing the wick to burn for a fixed period of time. Wicks were wrapped twice around the circumference of each burnt stem to ensure that intensity per unit area stem did not vary with stem size. The intensity of wick fire was calibrated by measuring fire intensities in high intensity fires burnt in the Pretoriuskop region of the Kruger National Park. These fires were burnt as part of the savanna fire ignition research experiment (SAV fire) on the 12th of June 2007 (Govender *et al* 2007). Hydropyrometers were used to measure intensities of both natural and wick fires. This was done by filling

aluminum cans attached to the hydrophyrometer with 20ml of water and measuring the volume of water evaporated by fires. Three hydrophyrometers were used to measure a natural fire of intermediate intensity. Each hydrophyrometer was fitted with four cans at ground level, grass canopy height and 1m above the ground. Intensities of wick fires burnt for a duration between 40 seconds and three minutes were measured using four cans for each time interval. This allowed us to generate a standard curve to calibrate the duration of a wick burn with natural fire's intensity (Fig. 1). The duration decided to most accurately replicate natural fire intensities was 2 minutes and 20 seconds. This was decided on the basis of intensities measured for both back and forward burns, at all height levels.

Allometry

The allometric relationships between plant size and defense mechanisms can be informative regarding resource allocation and the importance of certain selective pressures (Jackson *et al* 1999). The defense that we are interested in is bark thickness and the selective pressure is fire. The relationship between height and diameter is important in determining the relative importance of height and diameter in resisting fire damage. Measurements of stem diameter, bark thickness and plant height were taken for all stems included in experimental manipulations. These measurements were used to construct curves describing the allometric relationship between bark thickness and stem diameter as well as the relationship between stem diameter and plant height. Regression analysis was used to determine the pattern and strength of these allometric relationships.

Fire resistance and bark removal

Experimental treatments involving bark removal and burning of stems using wicks were set up between the 14th and 16th of June 2007. The purpose of these experiments was to explore stem resistance to fire-induced mortality and the effect of bark removal on resistance. Plants were chosen in the Rhino capture bhoma enclosure situated near Skukuza and in a communal area near Justicia, abutting Kruger National Park. Neither site had been burnt within the last two years prior to the start of the experiment. In order to determine thresholds of stem resistance in the absence of bark

removal 16 stems, with diameters ranging between 8 and 91mm were burnt using the wick burn technique. The effect of bark removal on stem mortality was determined by treating stems with three bark removal intensities: 30%, 60% and 100% of the circumference stripped. Bark removal comprised cutting roughly 5cm length of bark from the stem for all three treatments on stems ranging between 26 and 68mm. Half of the treated stems were burnt and the other half remained unburnt. Two unburnt, unstripped stems were included as controls. Sample sizes for each treatment are given in Table 1. Four months after treatments, survivorship of stems was determined by testing for living stem tissues above the burnt stem section. A 0.8% m/v solution of 2, 3, 5 triphenyl-tetrazolium chloride (TTC) in 0.05 mol/L potassium phosphate buffer was used as an indicator of respiration activity in tissues. TTC is reduced to insoluble pink formazan by living tissue but remains colourless in dead tissue, as shown in figure 2 (Roberts 1950). TTC has been used in numerous studies to examine heat impacts on stem tissues (Waugh 1948, Bova and Dickenson 2005, Jones *et al* 2006). Three bark samples were taken from around the circumference of each stem 10 cm above the burn scar and immersed in a dark chamber overnight in the TTC solution. Only if all three bark samples gave a negative result was it concluded that a stem had been killed. This is because it takes complete ring-barking to kill *Acacia nigrescens* stems (Moncrieff *unpubl. data*). Stem survival was compared to bark removal in order to determine the effect of bark removal on mortality.

Mechanisms of fire induced stem death

The effects of fire on stem cambium in *Acacia nigrescens* were investigated using TTC to determine mortality. Twelve unstripped and eleven 50% stripped stems were burnt using the wick technique. The following day stem sections roughly 5cm in length were cut from 2cm above the wick burn scar and immersed in TTC overnight. The proportion of the remaining cambium (i.e. 100% in unstripped and 50% in stripped stem) around the stem circumference that had not been killed by the fire was measured the following day. The proportion of cambium killed was plotted against stem diameter and separate logistic regressions were performed for the unstripped and stripped treatments using the following formula for logistic growth:

$$y = \frac{1}{1 + e^{-(a+bx)}}$$

The influence of bark stripping on the relationship between stem diameter and cambium survival was analyzed using ANCOVA implemented in Statistica® v7.

Elephant utilization and consequent fire induced topkill following natural fires

Saplings:

Field surveys of recently burnt (< six months) *Acacia nigrescens* stems were conducted in the Skukuza and Tshokwane districts on the Kruger National Park between the 2nd and 7th of October 2007. Small trees (< 15cm stem diameter) were surveyed in order to determine the pattern and strength of the relationship between stem diameter and topkill. Height, stem diameter and the post-fire fate (alive/dead) of all stems encountered in transects with a diameter less than 15cm at 10cm above the ground was measured.

Adults

Patterns of utilization and mortality in large *Acacia nigrescens* trees were investigated for all stems encountered in transects with a dbh greater than 15cm. For each large tree encountered the following was noted: stem diameter, height, presence or absence of bark stripping, the agent of bark stripping (porcupine or elephant), maximum percentage of the circumference stripped, total percentage of the circumference up to 3m stripped, the height of the lowest point of stripping, the age of stripping (as defined in table 2), charring of the xylem heartwood, the invasion of boring beetles in the heartwood and the post-fire fate (alive/dead) of the tree in question.

For small stems (<15cm), the proportion of topkilled stems in each size class was plotted. For the larger stems, the stem size distribution of bark stripping was determined by plotting the proportion of stems stripped against stem size. Size based patterns of utilization were investigated by plotting the mean maximum percentage of the

circumference stripped and the mean total percentage of the circumference up to 3m stripped against stem size. The proportion of stems was plotted against the intensity of stripping for both the maximum percentage of the circumference stripped and the total percentage of the circumference up to 3m stripped. Two-sample t-tests were used to test for differences in the mean percent of bark stripped for both total percentage of the circumference up to 3m stripped and the maximum percentage of the circumference stripped between trees that survived and those that were killed by fire.

In order to determine which variables best explain post-fire mortality patterns General Discriminant Analysis was implemented in Statistica® v7. This type of analysis is used to determine which categorical or continuous variables explain group membership. In our case the two groups of interest are dead stems and living stems. Stem diameter, height, maximum percentage of the circumference stripped, total percentage of the circumference up to 3m stripped and the height of the lowest point of stripping were used as continuous predictor variables. The agent of bark stripping (porcupine or elephant), charring of the xylem heartwood, the invasion of boring beetles in the heartwood and the age of stripping were used as categorical factors. Prior probabilities of classifications were estimated and the model was constrained to include all effects.

Table 1. Numbers of *Acacia nigrescens* stems burnt using the wick technique in the long term study of the interaction between bark removal and fire.

Stripping intensity	Unburnt	Burnt
0%	2	7
30%	4	7
60%	4	7
100%	2	3

Table 2. Classification and characteristics bark stripping age.

Age class	Defining characteristics
1	Fresh sap seeping from wound
2	No seeping sap, wound and xylem surface red in colour
3	Xylem surface grey
4	Xylem surface grey, evidence of boring beetles

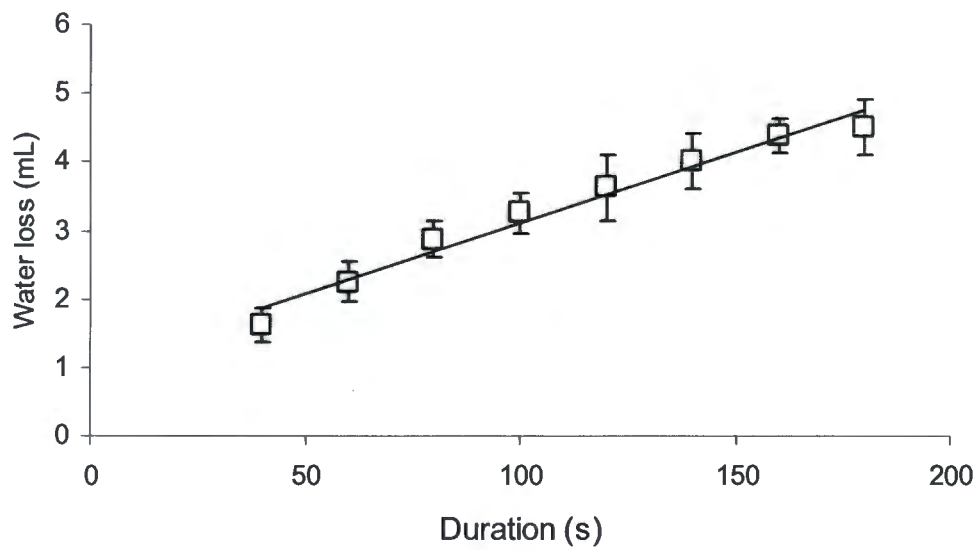


Figure 1. The intensity of fires burnt for different durations using the wick technique on aluminum can filled with 20mL of water. 140 seconds was chosen as the duration most accurately simulating savanna surface fires ($y = 0.0205x + 1.0536$, $R^2 = 0.97$, $n = 46$).

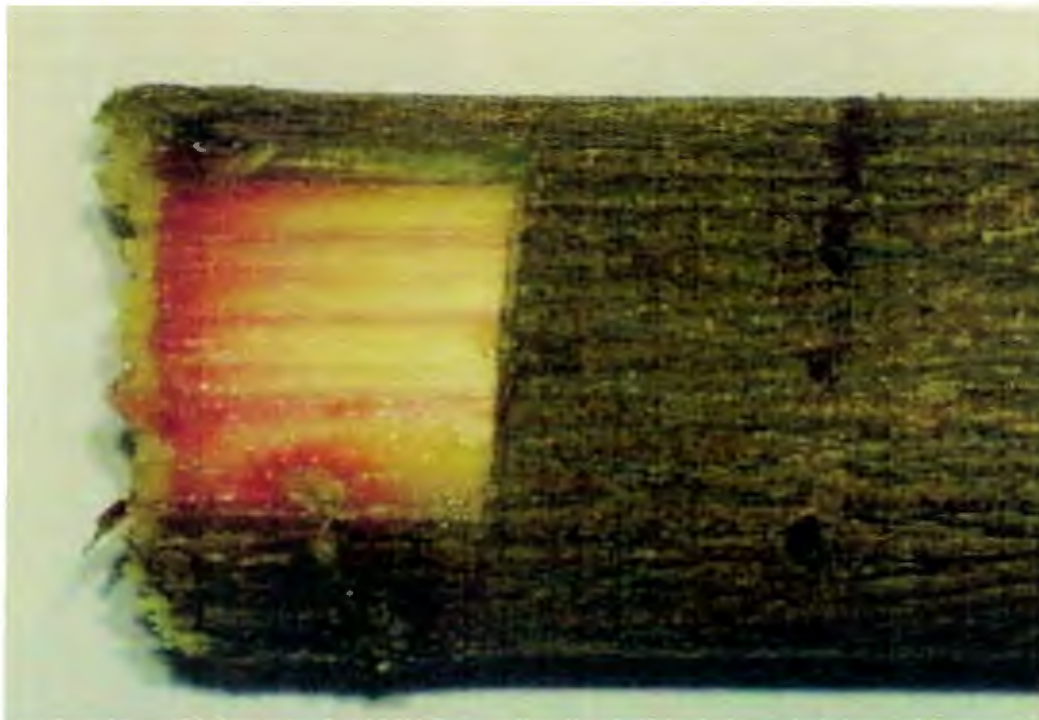


Figure 2. Stem cambium stained using TTC. The red colour indicates living tissue.

Results

Allometry

As expected, there is a strong relationship between stem diameter and plant height ($R^2 = 0.72$, $m = 0.679$, $p < 0.001$, Fig. 3) and the between bark thickness and stem diameter ($R^2 = 0.74$, $m = 0.928$, $p < 0.001$, Fig. 4). The allometric coefficient for the relationship between bark thickness and stem diameter is close to 1. This indicates that there is no early allocation to bark growth, as would be expected for savanna trees (Jackson *et al* 1999).

Experimental results

Regardless of the intensity of stripping, none of the unburnt stems had died after 4 months of exposure. In contrast, burnt stems did die, and the proportion of stems killed in each stripping intensity class increased with increasing stripping intensity ($m = -0.0053$, $R^2 = 0.85$, $p = 0.0094$, Fig. 5). For burnt stems, almost all stems with less than 60% bark removal survived, whilst survival rapidly decreases for the 60% and 100% bark removal treatments. Interestingly, for stems 100% stripped (ring-barked) only those that were burnt had died by the time stems were assessed. The frequency distribution of living and dead stems in the different types of treatments applied is shown in table 3.

All stems with diameters less than 5cm had 100% of their cambium circumference killed by the experimental fires (Fig. 6). As stem size increased, the proportion as cambium surviving increased linearly for both 50% stripped and unstripped stems ($a = -5.578$, $b = 0.0711$, $R^2 = 0.728$, $p < 0.001$ (stripped); $a = -6.652$, $b = 0.1037$, $R^2 = 0.791$, $p < 0.001$ (unstripped)). However, even the largest unstripped stem (88.2mm) still had a large proportion of its cambium killed (38%). The linearity of this relationship is due to the size range of stems treated, if larger stems were included the curve would most likely asymptote at 100% survival. Thus the use of a logistic curve is justified. Although it appears as though the proportion of the cambium circumference killed is

consistently greater in stripped stems, this relationship is not significant ($F=1.8396$, $d.f.=1$, $p=0.19$), though the effect of stem diameter size is ($F=63.77$, $d.f.=1$, $p<0.0001$).

Field surveys

The proportion of stems topkilled in each diameter class is shown in figure 7. The total number of small stems surveyed was 148, of which 93 (62.8%) were alive and 55 dead (37.2%). It appears as though a threshold value is reached between 4 and 5cm diameter above which most survive topkill. In total 437 large trees were surveyed ranging from 15 to 85 cm in diameter. Of the surveyed trees, 22 (5%) were found to have been killed by the fire, while 415 survived (95%). All dead trees, save one, had been stripped either by elephants or porcupines. In total 196 (44%) trees were found to have had bark stripped by elephants, whereas 14 (3%) were judged to have been stripped by porcupines. The mean maximum percentage of the circumference stripped was 66.2% for dead trees and 30.1% for surviving trees. The mean total percentage of the stem stripped up to 3m was 51.4% for dead trees and 17.3% for surviving trees. The mean maximum percentage of the circumference stripped was significantly greater for dead trees than surviving trees ($t=-5.67$, $d.f.=23$, $p<0.0001$) as was the mean total percentage of the stem stripped up to 3m ($t=-4.74$, $d.f.=22$, $p<0.0001$). The size class distribution of bark stripping on stems is shown in Figure 8. There is a general linear trend of an increasing proportion of stems with bark stripping with increasing size. The overall pattern is of a very high proportion of stems being stripped, with 69% of all trees larger than 50cm stem diameter experiencing some degree of bark stripping. The mean percent of bark removed per size class increases as the size of stems increases for both maximum percentage of the circumference stripped and the total percentage of bark removed up to 3m (fig. 9). The proportion of stems stripped in each stripping intensity class decreases for higher stripping intensities for both measures of stripping (fig. 10). Of all the variables incorporated into the General Discriminant Analysis, only the total percentage of the circumference up to 3m stripped significantly discriminated between alive and dead stems ($F=7.57$, $d.f.=1$, $p=0.0076$).

Table 3. Mortality patterns of *Acacia nigrescens* stems burnt using the wick technique in the long term study of the interaction between bark removal and fire.

Stripping intensity	Unburnt		Burnt	
	Dead	Alive	Dead	Alive
0%	0	2	1	6
30%	0	4	1	6
60%	0	4	2	5
100%	0	2	2	1

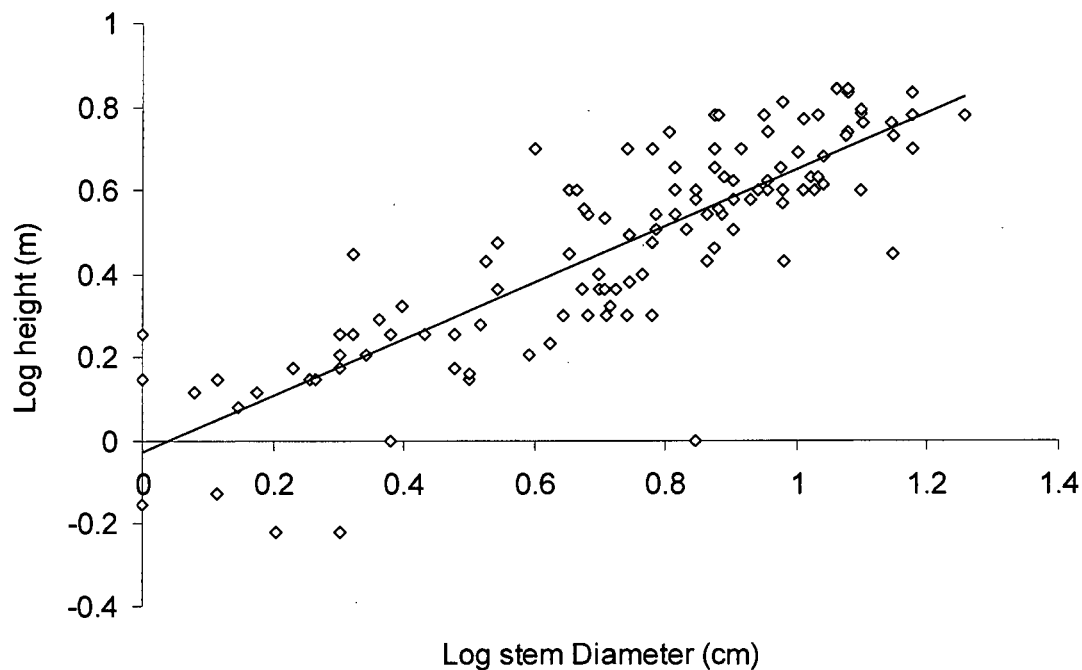


Figure 3. The relationship between stem diameter and stem height for *Acacia nigrescens*. Both axes are log-transformed. ($y = 0.6792x - 0.0255$, $R^2 = 0.72$, $n = 125$).

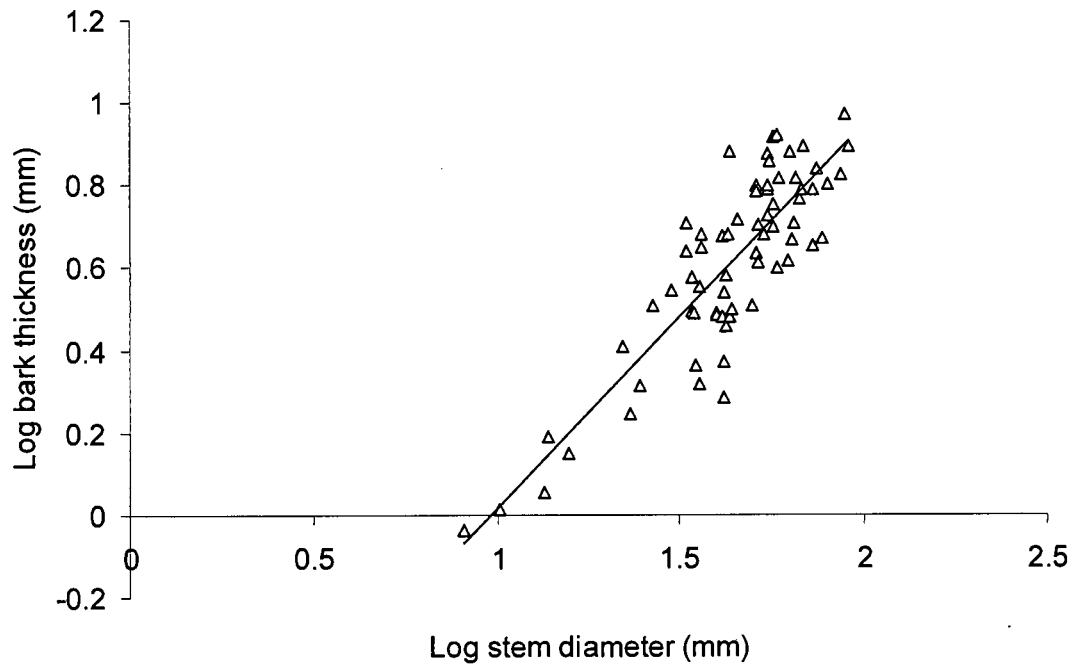


Figure 4. The relationship between stem diameter and bark thickness for *Acacia nigrescens*. Both axes are log-transformed ($y = 0.928x - 0.9125$, $R^2 = 0.74$, $n = 68$).

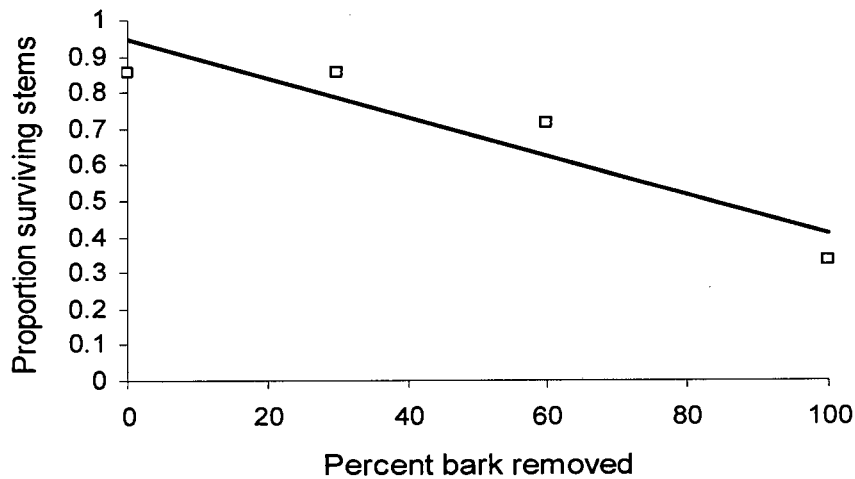


Figure 5. The relationship between the percent of bark removed around the circumference and stem survival of *Acacia nigrescens* ($y = -0.0053x + 0.9446$, $R^2 = 0.85$, $n = 24$).

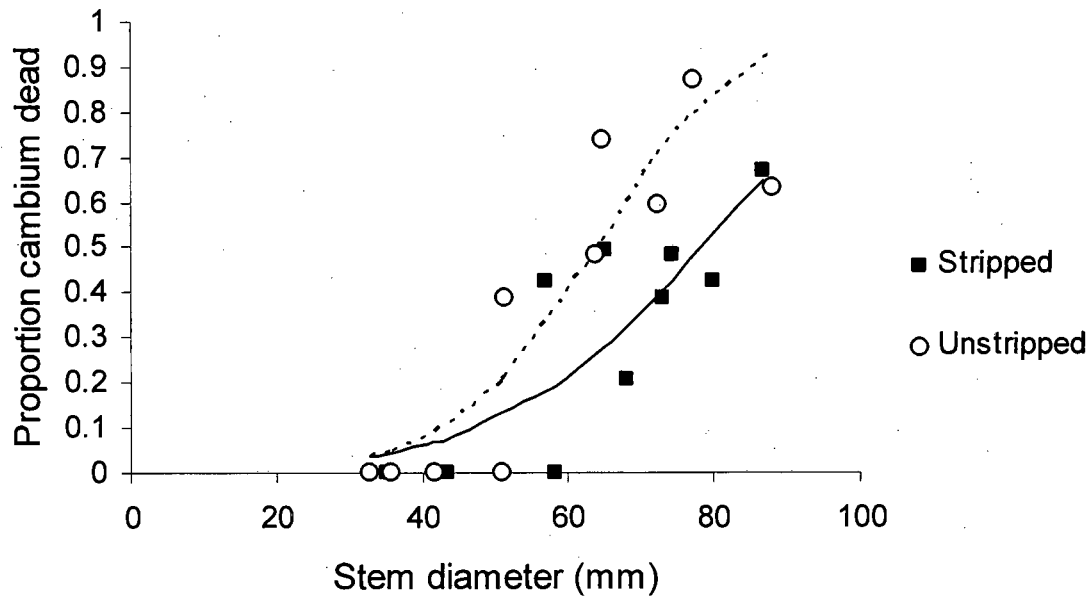


Figure 6. The proportion of cambium around the circumference killed by wick burns plotted against stem diameter for both unstripped and 50% stripped stems. The solid represents the regression for 50% stripped stems ($y = 1/(1+(\exp(-(-5.578+0.0711x))))$), $R^2 = 0.728$, $n = 12$) while the dashed represents the regression for unstripped stems ($y = 1/(1+(\exp(-(-6.652+0.1036x))))$), $R^2 = 0.791$, $n = 11$).

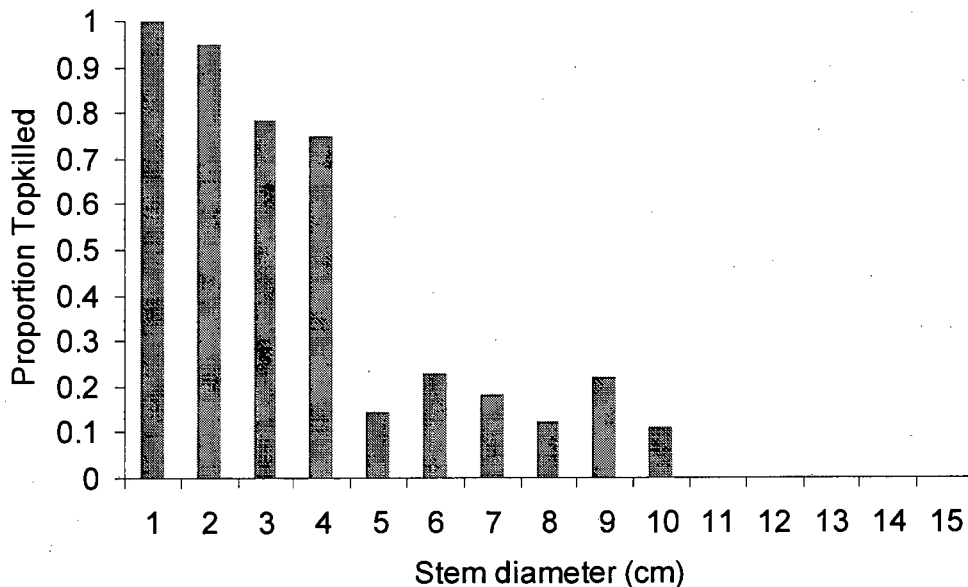


Figure 7. The proportion of *Acacia nigrescens* stems with a stem diameter less than 15cm topkilled by natural fire ($n = 148$).

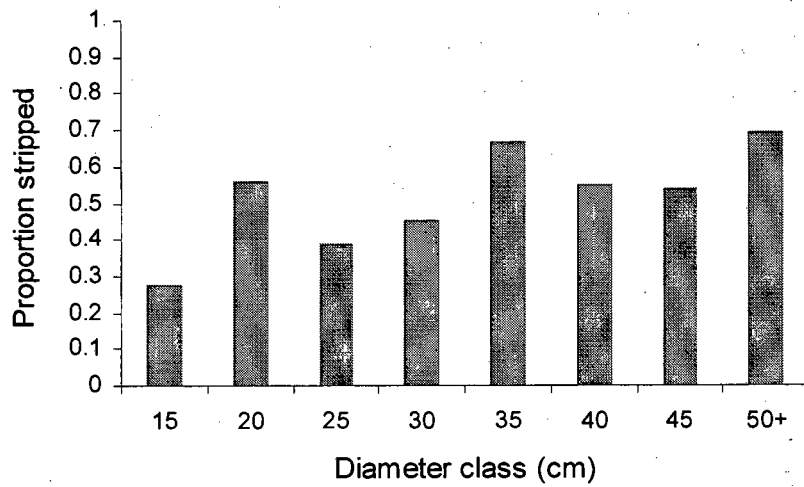


Figure 8. The size based distribution of elephant bark stripping on *Acacia nigrescens* stems with a stem diameter greater than 15cm (n = 210).

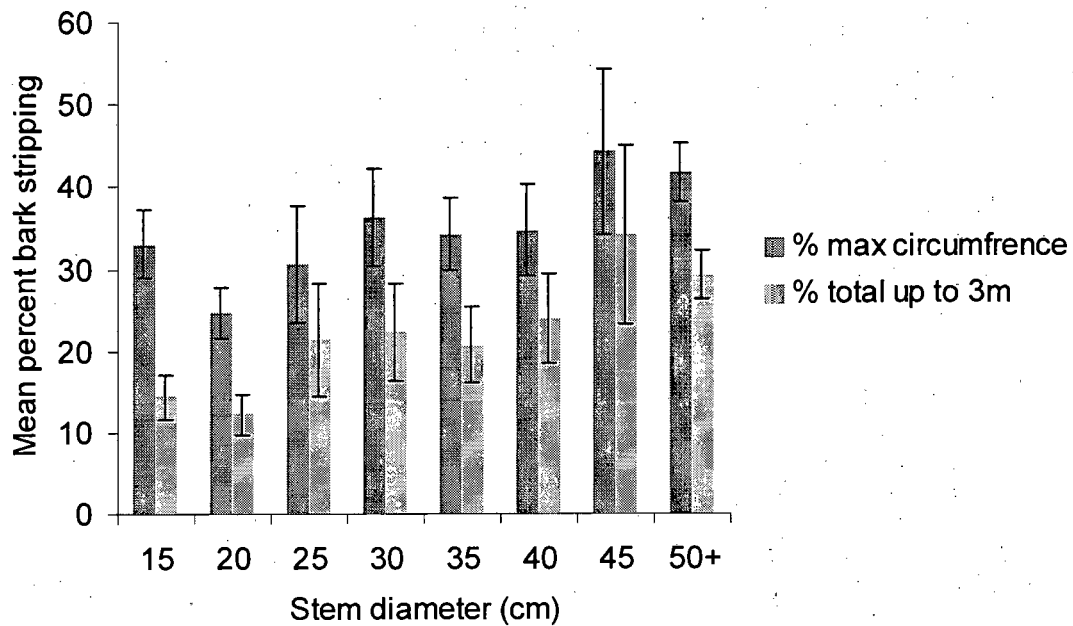


Figure 9. The mean percent of bark removed from stripped *Acacia nigrescens* stems with a stem diameter greater than 15cm (n = 210).

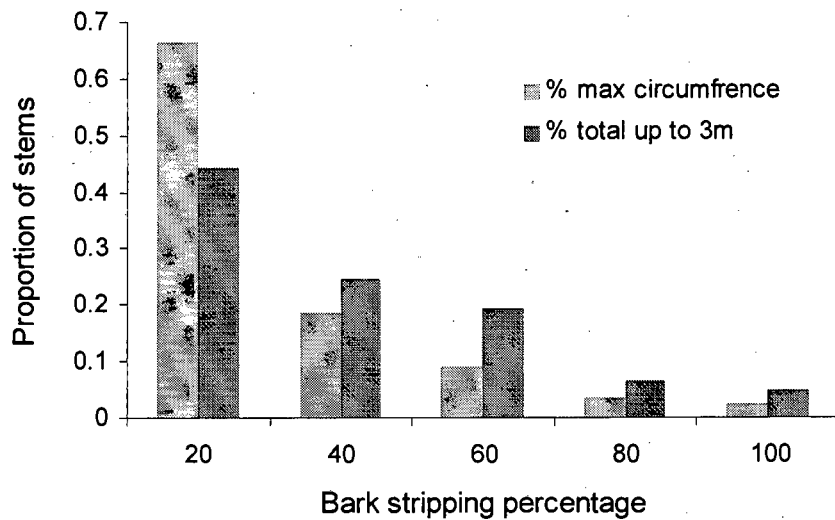


Figure 10. The distribution of bark stripping intensity for all stripped *Acacia nigrescens* stems with a stem diameter greater than 15cm (n = 210).

Discussion

Mechanistic insights

The threshold stem size for fire survival appears to be around 4-5cm (Fig. 7), this corresponds to a height of approximately 2m which is roughly the escape height of trees from canopy scorch (Bond and van Wilgen 1994). This appears to suggest that plant height is the critical determinant of fire survival. However, most stems below this height were completely topkilled and will thus have to resprout from the base of the stem. Balfour and Midgley (2006) showed that *Acacia karroo* stems that had only their canopy scorched resprouted from epicormic buds in the canopy and not from the base of the plant. Only when stems were burnt did plants resprout from the base. Stem damage is therefore more important than plant height in determining fire survival.

The allometric coefficient of the relationship between bark thickness and stem diameter is surprisingly low. This suggests that there is less allocation to bark growth in saplings than expected (Jackson *et al* 1999). A possible explanation for this is that the bark thickness of large stems was overestimated. This is possible because the bark of large *Acacia nigrescens* stems is of very low quality and deeply fissured and furrowed. The

higher quality of bark on small stems suggests higher allocation than is reflected by the allometric relationship.

Upon initial inspection of the results it appears as though patterns of post-fire stem mortality are well explained by heat damage inflicted to the stem cambium. This is because threshold stem size for fire survival (4-5cm) is also the stem diameter below which all stems had 100% of their cambium circumference killed by fire. This may be true, but when cambium was removed by bark stripping (resulting in cambium death as would occur in fires) no trees died, even after 4 months and with complete ring-barking. Only when trees were stripped and subsequently burnt did rapid topkill occur. The only additive effect that burning can have in this case is to damage the xylem, as all the phloem and cambium have been removed (at least in the 100% stripping treatment). Thus the mortality patterns observed in the field studies would not be manifest as rapidly as observed if only cambium and/or phloem damage was important in determining mortality. However, because it is safe to assume that all trees with 100% of their cambium circumference have a high probability of eventual topkill, it is possible that the same patterns of mortality would be evident in the longer term if only cambium and/or phloem were of importance. This does not detract from the role of xylem damage in hastening mortality. Balfour and Midgley (2006) showed that fire induced xylem damage resulted in leaf loss after fire in *Acacia karroo*, but the results presented here are the first evidence that fire-induced xylem damage affects stem mortality. It is likely that heating of the water traveling in xylem vessels induces embolisms resulting in the cavitation of conduits. This hastens mortality as the stem would be under increased transpirational and nutritional stress if its conduits were embolized (Tyree and Sperry 1988).

The means through which cavitations are seeded may be different for embolisms induced by fire as opposed to embolisms induced by drought stress. Increased tension in the water column caused by drought stress is said to result in embolism of vessels by the seeding of air bubbles from adjacent, embolized conduits through vessel wall pores (Tyree and Sperry 1988, Tyree *et al* 2000). The spontaneous nucleation of air bubbles is thought not to be a major cause of cavitation (Tyree and Sperry 1988, Tyree *et al* 2000).

Heating of the water within a conduit does not seem to be a likely cause of increased tension within the water column, thus it may not increase the likelihood of the introduction of embolisms in the tradition manner. However, because Henry's law states that gas solubility decreases as temperature increases, heating may increase the probability of the spontaneous nucleation of air bubbles, in the worse case scenario causing the water in a conduit to boil.

The removal of bark by elephants increases both the vulnerability of cambium to fire damage and the vulnerability of xylem. Obviously the removal of bark reduces the amount of cambium surrounding the stem circumference, and this will increase the probability of stem mortality, but it is the interaction between bark stripping, fire and stem mortality that is the subject of this study. Fire-induced topkill (or stem mortality) is what we are attempting to explain. Although the difference in cambium survival between stripped and unstripped trees was not significant, a greater proportion of the cambium circumference is killed by fire in stripped trees (Fig. 3). The non-significance of this result is most likely a result of low statistical power. Because bark removal increases the vulnerability of cambium to fire, trees that would otherwise have thick enough bark to protect a high enough percent of their stem cambium from fire to survive will become vulnerable to fire induced mortality. This mechanism explains how trees that would otherwise be resistant to topkill become vulnerable due to elephant utilization, thus explaining the observed pattern of death occurring in very large trees. Two possible explanations exist for the increased vulnerability of cambium to fire damage as a result of bark stripping. The removal of bark may expose the cambium immediately adjacent to the stripped area to fire. Without bark adjacent to it, cambium will become vulnerable to lateral heat transfer from fire burning at the interface of stripped and unstripped stem surfaces. Heat transfer through the stem has been suggested to play a role in causing cambium death (Uhl and Kaufmann 1994, Gignoux *et al* 1997). If this is true, then bark removal will substantially increase the likelihood of cambium killed being by fire through the elimination of the insulation provided by the bark on the opposing side of the stem. Bark stripping will clearly increase the amount of damage caused to xylem through the removal of insulation. As was shown the long term experimental treatments, xylem

damage does play a role in post-fire stem mortality. It also appears as though as more xylem is exposed through increasing intensities of bark removal so the probability of mortality increases.

Natural mortality patterns

Bark stripping by elephants on *Acacia nigrescens* a prominent occurrence in the Kruger National Park, far more frequent than bark stripping by porcupines. However, most instances of bark stripping are of a low intensity. As was found for *Acacia tortillis* and *Acacia nilotica* by MacGregor and O'Conner (2004) and for *Sclerocarya birrea* by Gadd (2002), bark stripping is accumulated by the largest stems. Therefore the largest trees are particularly vulnerable to the ancillary effects of bark stripping. The results confirm that bark stripping strongly influences post-fire survival of large stems, as all trees killed by fire had had bark stripped, with a significantly greater proportion removed than those that survived fires. The overriding importance of bark stripping in determining stem survival is further emphasized by the fact that stem size was not useful in discriminating between dead and surviving stems, while the total percent of bark removed up to 3m was. Bark regrowth does not appear to be fast enough to compensate for elephant utilization, as large tree accumulate stripping, rather than recover from it. Demographic studies are needed in order to determine if replacement rates are high enough to compensate for the high mortality rates of stems after fire (ca. 5%) as a result of elephant utilization.

It is interesting that only the total percent of bark removed up to 3m is useful in discriminating between dead and surviving stems, while the maximum percent of the circumference stripped is not. One would expect the maximum percent of the circumference stripped to be of importance if cambium or phloem survival is important in determining post-fire mortality, as this variable is a measure of how close the stem is to being ring-barked. The total percent of bark removed up to 3m can be thought of as a measure of the total surface of xylem exposed to directly to fire. This provides further evidence suggesting elephants render large trees vulnerable to fires by exposing their xylem.

The exposure of heartwood to burning and the subsequent mechanical failure of stem support as a result of successive burning, proposed by Yeaton (1988) as a mechanism resulting in the death of large stem, does not appear to be important in the mortality of large *Acacia nigrescens* stems. The scarcity of porcupine damage and the non-significance of damage to heartwood in determining mortality imply that the importance of this mechanism of mortality has been overestimated. Rather, the frequency of elephant stripping and its importance in determining post-fire survival suggest that the importance of bark removal by elephants in the mortality of large trees has been underestimated.

Conclusions

The importance of bark stripping in determining fire survival, combined with the observation that bark stripping is most prevalent and intense in large stems affirms the role played by elephants in post-fire mortality patterns of large *Acacia nigrescens* trees. In order to prevent the loss of these sentinels of the savanna landscape the utilization of trees by elephants in the form of bark stripping needs to be mitigated. Large trees have an important role to play in savanna ecosystem. They act as nutrient and water pumps, enhancing productivity below their canopy (Ludwig *et al* 2004). They also provide shade and roosts for various bird and mammal species, further enhancing the nutrient status of the surrounding soils as a result (Dean *et al* 1998). Thus the threat posed by elephants to large trees is not to be taken lightly. Current patterns of utilization and mortality appear unsustainable and action must be taken in order to prevent long-term ecosystem changes from taking effect. The effect of current utilization by elephants will resonate for years to come in the form of interactions between damage left behind and subsequent fires. Thus proactive steps are required from park managers that will swiftly and effectively reduce elephant impacts to sustainable levels.

Larger scale patterns of bark stripping, incorporating comparisons across productivity and rainfall gradients and multiple species, need to be investigated in order to understand variation in patterns of utilization. It is clear that fire-induced xylem

damage plays a major role in post-fire stem mortality and mediation of elephant-fire effects on stem survival. Mechanistic insights into how heat damage is manifested are required in order to determine critical levels of damage. Little is known about the influence of heat in the functioning of xylem vessels and how it may cause the cavitation of conduits. Despite the apparent negative effects of elephants and fire on *Acacia nigrescens* and the woody vegetation of savannas in general, both are essential components of in the ecosystem.

Acknowledgements

This research would not have been possible without the assistance provided to me by the Organization for Tropical Studies. Jon Aronson, Sarah Lupton, Phoebe Poole, Vere Ross-Gillespie, Lexie Sabella and Linan Xiao contributed to my ideas through collaboration in associated projects. Navashni Govender and Dr. Winston Trollope allowed me to collect data during their experiments and provided insightful comments and discussions. Tim Aston provided helpful discussions regarding staining techniques. I am enormously grateful for the assistance and support, both moral and financial, given to me by Dr. Laurence Kruger and A/Prof Jeremy Midgley. Your enthusiasm has been infectious and I hope to spread the infection to all those I work with in years to come.

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