Plant fire defence strategies, topkill responses and change in vegetation structure in the Kruger National Park

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Abstract

Fire is important in structuring savanna vegetation. In this study growth patterns of eight plant species impacted by fire in the Kruger National Park were assessed to determine the relationship between bark thickness, tree height, stem diameter and topkill. With the exception of *Dichrostachys cinerea,* species initially invest more in bark thickness than in their stem diameters. There were varied relationships between growth in height and stem diameter for the different species. The study then investigated whether plant height, fire season and fire intensity significantly contribute to variation in topkill response in these species. Topkill in *Acacia nigrescens, Dichrostachys cinerea, Terminalia sericea* and *Philenoptera violacea* is significantly affected by all three variables, whereas for *Colophospermum mopane* and *Sclerocarya birrea* it is not significantly affected by fire intensity. In *Combretum imberbe* and *C. apiculatum* topkill is not significantly influenced by season of burn. Models based on these results generated topkill probabilities for each species and these were compared to average bark thickness and moisture content. Although only significant at the 10% level, the data suggest that thicker bark and higher bark moisture content reduce a plant's probability of topkill. The ability of the models to predict change in vegetation structure was tested using long-term data sets from Kruger. For *A. nigrescens, C. imberbe, D. cinerea, T. sericea* and *P. violacea*, when the probability of not being topkilled was low the proportion of tall trees increased over time. At higher probabilities of not being topkilled there were greater proportions of small trees in later surveys. It is suggested that when the probability of not being topkilled is low only trees tall enough to be unaffected by fire persist, whereas at higher probabilities more small individuals occur. There was not a significant relationship between change in vegetation structure and topkill response for *C. mopane*. This study identified traits which increase plants' resistance to fire and showed that topkill response can predict changes in vegetation structure for certain species. Future work is needed to ascertain why topkill response does not explain vegetation structural changes in *C. mopane.*

Introduction

Whilst vegetation composition and structure in savannas are influenced by a number of factors, fire is recognised as one of the most ubiquitous forms of disturbance in these

systems (Bond and van Wilgen 1996; Abbadie *et al.* 2006; Govender *et al.* 2006). Savanna structure ranges from scrubland to closed woodland over broad geographical scales. An important question that has often been posed is why savannas differ in woody vegetation structure (Belsky 1990). One hypothesis is that below a mean annual precipitation of 650 mm per year, fire and herbivory do not significantly contribute to woody vegetation structure (Sankaran *et al.* 2005). However, in areas where rainfall exceeds 650 mm, vegetation structure is more heavily influenced by fire and herbivory. Enslin *et al.* (2000) found that changes in woody vegetation in response to fire are more likely to be transformations in structural diversity than shifts in species diversity and composition. They suggest that in the Kruger National Park in South Africa, the woody vegetation is being transformed by fire into low canopied woodland communities, with the occasional tall tree. Fire is often termed a "megaherbivore" and only elephants and other animals which feed on bark can influence vegetation structure to the same extent (Bond and van Wilgen 1996).

The role of fire in vegetation structure and topkill

Fire intensity has an important influence on tree establishment and is linked to tree mortality (Govender *et al.* 2006). Bond and van Wilgen (1996) coined the term, the "Gulliver effect", which describes the establishment of trees in savannas. They suggest that savanna "Gullivers" are multi-stemmed shrubs less than 3 m tall susceptible to mortality from fire, caught in the herbaceous layer which they call the "fire trap". They observe that the herbaceous layer tends to suppress the recruitment of "Gullivers" while also generating fuel for fires. In order to escape the fire trap, young trees have to survive within the herbaceous fuel bed where fire intensity is highest (Abbadie *et al.* 2006). Trees are prevented from reaching maturity by recurrent fires which kill above ground biomass through a process termed "topkill" (Bond and van Wilgen 1996). Individual "Gullivers" may, however, persist within the herbaceous layer for many years, often resprouting from a well-established root system (Bond and van Wilgen 1996). If "Gullivers" are able to survive and grow above the herbaceous layer the vegetation structure may change rapidly into woodland.

Circumstances that allow trees to escape the fire trap may be linked to the grass component being removed by fire and grazing (Bond and van Wilgen 1996). The "Gulliver" hypothesis (Bond and van Wilgen 1996) is used to explain the life history traits of tree species such as *Acacia nigrescens*, but is not necessarily true for other trees. Gignoux *et al.* (1997) found that some species employ a strategy of quick re-growth of above ground structure in the form of a single thin pole after fire, whilst others continuously invest in developing resistance to fire of above ground structures. The season that fires occur in is thought to be significant. Trees and shrubs are likely to be more susceptible to fire mortality if fires occur at the end of the dry season when reserves are low as they have been investing in new spring growth (Enslin *et al.* 2000).

Plant adaptation to fires and allometric growth patterns

Bond and van Wilgen (1996) suggest that one of the most essential determinants for survival is bark thickness rather than other bark properties. Uhl and Kauffmann (1990) however state that bark moisture content may also significantly influence the thermal insulation of the stem's living tissue. Trees have to invest equally in bark thickness and stem height to escape the fire trap. Increased investment in defence traits may however result in a corresponding trade-off in reducing the amount of resources allocated to growth in stem diameter (Sumida *et al.* 1997; Jackson *et al.* 1999).

In this study I investigate the fire resistance strategies employed by *Acacia nigrescens*, *Colophospermum mopane*, *Combretum apiculatum*, *Combretum imberbe*, *Dichrostachys cinerea*, *Sclerocarya birea*, *Terminalia sericea* and *Philenoptera violacea* growing in the Kruger National Park in the north of South Africa. These eight species are dominant over a wide area in the Park and their response to fire and resulting changes to their height structure have significant effects on the structure of the landscape. Here I explore how each of these species invests in bark thickness over stem growth and in increasing height as opposed to stem diameter. Using data collected over a number of years, I analyse the relative importance of fire intensity, plant height and fire season in determining the topkill response for individual plants of each species. I then generate topkill probability values for 2 m tall individuals, exposed to a fire with a standard intensity and season and

test whether bark thickness and bark moisture content may influence the probability for survival. I assess how well the topkill models for each of the tree species used in this study relate to actual population responses to fire and whether this has a bearing on the resulting vegetation structure in Kruger National Park. I generate a predictive index of topkill of the average probability of an individual in specific landscapes not being topkilled for three years. This was compared to the change in size class dominance between surveys conducted in 1954 and recent surveys from 2002 to 2006. I then test to see whether the species specific topkill models are more effective at predicting the change in vegetation structure than simply attributing change in height structure to average fire intensity.

Methods

Study sites

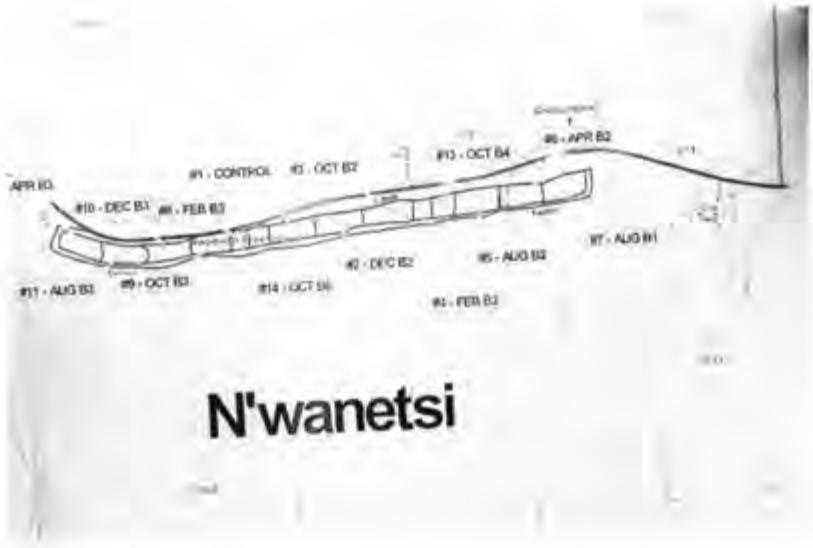
The data used in this project were collected in different years from the experimental burn plots (EBPs) in the Kruger National Park in the north of South Africa (Fig. 1a). The EBPs were demarcated in 1954 to determine the effects of fire frequency, intensity and season of burn on vegetation structure in the Kruger Park. They consist of randomised treatments which differ in season and frequency of burn and comprise of: fire exclusion (control) and annual, biennial and triennial fires in August (winter), October (summer), December (summer), February (summer) and April (winter) (Van der Schijff 1958 cited Biggs *et al.* 2003; Govender *et al.* 2006). The treatments are replicated four times in four landscapes at Mopani, Satara, Skukuza and Pretoriuskop (Table 1, Fig. 1a and 1b). Not all of the combinations of fire season and frequency are used in all of the replicates. Each plot within the different replicates is approximately 360 m by 180 m, which is roughly 7 ha in size (Enslin *et al.* 2000).

Table 1. Outline of the main features of each of the four landscapes that the experimental burn plots are situated within in the Kruger National Park, South Africa (adapted from Trollope and Potgieter 1985; Enslin *et al.* 2000; Biggs *et al.* 2003; Govender *et al.* 2006).

Landscape	Major vegetation type and general structure	Geology	Mean annual rainfall (mm)	Altitude (m)
Mopani	*Colophospermum mopane* savanna. Dense and low (1-2 m).	Basalt	447	300 – 340
Satara	*Acacia nigrescens /Sclerocarya birrea* savanna. Scattered tall (10-15 m) trees.	Basalt	544	240-320
Skukuza	*Combretum collinum /Combretum zeyheri /Acacia nigrescens* savanna. Dense and medium height range.	Granite	550	400-480
Pretoriuskop	*Terminalia sericea* lowveld sour bushveld. Dense and tall (10-15 m).	Granite	737	560-640

(a)

Fig. 1. (a) Location of the Kruger National Park in the north of South Africa and the location of the four landscapes of Mopani, Satara, Skukuza and Pretoriuskop in which the experimental burn plots are situated.



(b)

Fig. 1. (b) An example of the layout of the experimental burn plots in the N'wanetsi string in the Satara landscape.

Growth patterns and allometry

The first part of the analysis assessed allometric growth patterns in an attempt to determine the relationship between tree height, bark thickness and stem diameter. The height and stem diameters of individual plants were recorded by the University of Cape Town (UCT) Tree and Grass Programme from 2002 to 2005 at Satara and Pretoriuskop. Andre Potgieter (KNP Scientific Services) collected height and stem data from Mopani and Skukuza in 1970 and William Sea (University of Colorado) in Mopani and Skukuza in 2004. I used these data sets to examine the relationship between height and stem diameter. To assess the relationship between stem diameter and bark thickness I combined data I collected for diameters and bark thicknesses in 2006 with data on bark thickness and stem diameters collected by UCT in 2005.

Both stem diameters and bark thickness were determined at breast height for a range of different size classes. Bark thickness was determined by excising a segment of bark roughly 5 x 10 cm at a height of approximately 1.5 m and measuring the thickness with callipers. Based on the study by Kayll (1963) the heat transfer that occurs on the thickest part of the bark as opposed to the thinnest is the limiting factor in determining the effect of fire. Three measurements of bark thickness were recorded and the highest value was

used in the analysis. The general growth patterns of species were assessed through regression analyses of bark thickness against stem diameter and stem diameter against tree height. The regression function (linear, power or exponential) which offered the best fit by minimising the sum of squared deviations was selected as the best depiction of the overall growth pattern of the different species (Zar 1999).

When power functions offer the best fit to the data it is possible to assess the intraspecific allometric allocations to bark thickness and height over increasing stem diameter using the equation $y = bx^{\alpha}$. This provides a description of the relationship between bark thickness and height (y) relative to diameter (x) (Jackson *et al.* 1999). The allometric coefficient, α, provides a measure of the increase in stem diameter relative to bark thickness or height. If α is less than one, there is negative allometry with plants initially investing disproportionately more into developing thicker bark or gaining height over growing thicker stem diameters. If α is equal to one, there is an equal investment in bark thickness or height and in increasing stem diameter, and this is termed isometry. When α is greater than one, plants will delay investing in bark thickness or height in preference for thicker stems. This is known as positive allometry.

Topkill response of plant species

Data collection. The primary data set on topkill response was collected by the Tree Grass Programme of the UCT from 2002 to 2005, and Winston Trollope in 1987 on the fire plots in the four different landscapes. The response of the trees to different treatments (variation in intensity and season and frequency of the burn) was measured three months after fires had occurred to allow the vegetation adequate time to recover (Trollope *et al.* 1995). The response of individual plants were recorded along two transects along the centre of each of the halves of the burn plots. At 15 m intervals the topkill response and height of the closest plant species were recorded. The topkill response was defined as whether or not the plant had experienced canopy mortality in the previous fire (Bond and van Wilgen 1996). The first and last 20 m of the transects at the plots' peripheries were excluded. In addition to the topkill response and heights of the different plant species, the

intensity of the last fire and the season of burn of each of the burn plots were also recorded.

Calculating Fire Intensity. Data on fire intensity for the different years were provided by N. Govender, the fire ecologist in Kruger Park. The Byram's (1959 cited Govender *et al.* 2006) fire-line intensity equation used for calculating the fire intensities is

$$\mathbf{I = Hwr}$$

where fire intensity, **I** (kWm^{-1}), the rate at which heat energy is released from a fire (Trollope and Potgieter 1985), is dependent upon: **H**, the heat yield (kJg^{-1}); **w**, the mass of fuel burnt (gm^{-2}) and **r**, the rate of spread of the head fire front (ms^{-1}) (Govender *et al.* 2006). This particular equation for fire-line intensity is used as it has been shown to be strongly correlated with topkill in woody plants (Govender *et al.* 2006).

Logistic regression models of topkill response. Topkill in trees in the different burn plots in Kruger was analysed by making topkill a binary response (Crawley 2005). Logistic regression models with binomial errors were fitted using the variables of height, season (month) of burn and the intensity of the fire to the data on topkill response for all of the species used in this study. For *Acacia nigrescens* only the data collected by Trollope were used, whereas for the other species data collected by Trollope and UCT were incorporated into the analysis. This was due to sampling errors within the UCT data for *A. nigrescens.* A change in deviance test was used to ascertain whether height, season of burn and fire intensity contribute significantly to topkill. The significance of each of these variables was tested by deletion of terms from the main model and testing whether the changes in deviance were significant, assuming the deviances are chi-square distributed (Crawley 2005).

Role of bark thickness and bark moisture content

The bark thickness and the percentage moisture content of the bark were ascertained for 15 individual *Acacia nigrescens, Combretum apiculatum, Combretum imberbe,*

Dichrostachys cinerea, Sclerocarya birrea, Terminalia sericea and *Philenoptera violacea* plants of approximately 2 m in height at Skukuza, Satara and Pretoriuskop (Fig. 1). Sections of bark approximately 3 x 5 cm were cut out of the tree stem at breast height. After the bark thickness was measured the sample was weighed and then placed in an oven set at 50°C for 48 h. The bark sample was then re-weighed and the change in mass was calculated to give moisture content. To determine whether thicker bark and a high moisture content have an effect on topkill the average bark thickness and bark moisture content for the fifteen individual trees were plotted against the probability of a tree being topkilled when exposed to August fires with an intensity of 2000 kWm^{-1}. The probability was generated from August fires as this is the modal month for burning in Kruger (Govender *et al.* 2006). The average fire intensity for the different seasons is approximately 2000 kWm^{-1} (Govender *et al.* 2006) and this value was therefore used in calculating the topkill probabilities.

Predicting structural response of vegetation from topkill models

This part of the analysis aimed to ascertain whether the topkill models predict the changes in vegetation structure observed between surveys conducted on the experimental burn plots in 1956/7 (Time 1) and 1996-1999 (Time 2). The initial survey in 1956/57 recorded the size-class and species along two transects (2 m x 500 m wide) on each experimental plot but did not record height. In the second subsequent field study from 1996-99 height was recorded along with the size-class and species names. The second survey's data were used to randomly assign heights to the specific size classes of the first survey. Extreme outliers were not included as only heights falling within the 95% confidence interval were selected.

A topkill index (Higgins *et al.* submitted) was generated for each plot to verify predictions from topkill models for change in vegetation structure on the burn plots. This index is the mean probability of individual trees not being topkilled for 3 years on each burn plot in the various landscapes and is calculated from

$$T = \frac{1}{n}\sum_{i}^{n}[1 - p(h_i, I_j, S)]^{1/F}$$

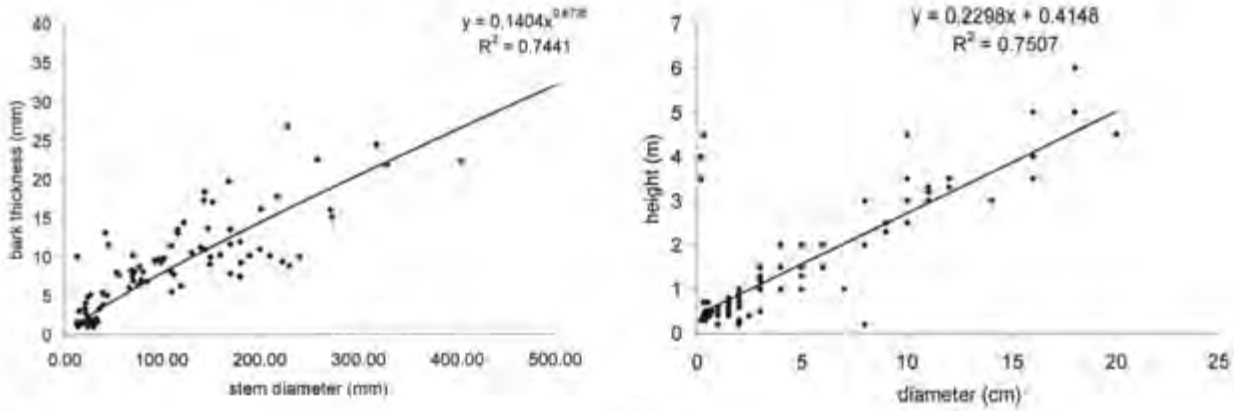
where n is the number of bootstrapped samples for which the mean is calculated (in this case 10 000 bootstraps; the index was only calculated if there was a minimum of 200 individual trees of a species in the data sets for each landscape); p is the species specific logistic regression model of topkill, which determines the probability of topkill in relation to fire season S and height h_i of the ith individual in a fire of bootstrapped fire intensity I_j. The topkill models are species dependent however, and as seen in the results, not all of the species had all three variables incorporated into their models. The tree heights h_i were bootstrapped from the distribution of heights generated for the initial survey in 1956/7. The fire intensity data for the experimental burn plots (Govender *et al.* 2006) were used to generate an empirical probability distribution of fire intensities for each treatment for the respective four landscapes. I_j is drawn from the empirical probability distribution and F is the different fire return intervals of 1, 2 or 3 years which are used in the different treatments.

The topkill index (T) for each species in each burn plot was then plotted against a value calculated for the change in the proportion of small sized individuals to the total number of trees of a species in the burn plot (change in dominance). This value is the ratio of the number of individuals less than 2 m high compared to the total number of trees in each burn plot for Time 2 (1996-99) subtracted from the ratio for Time 1 (1956/7). Topkill probability and change in dominance was compared with change in dominance and fire intensity for each burn plot. The primary objective for this was to determine the extent to which the species specific logistic regression models give a realistic picture of structural changes than simply fire intensity. The relationships between topkill index and change in dominance and between change in dominance and fire intensity were assessed through regression analysis.

Results

Growth patterns and intraspecific allometry

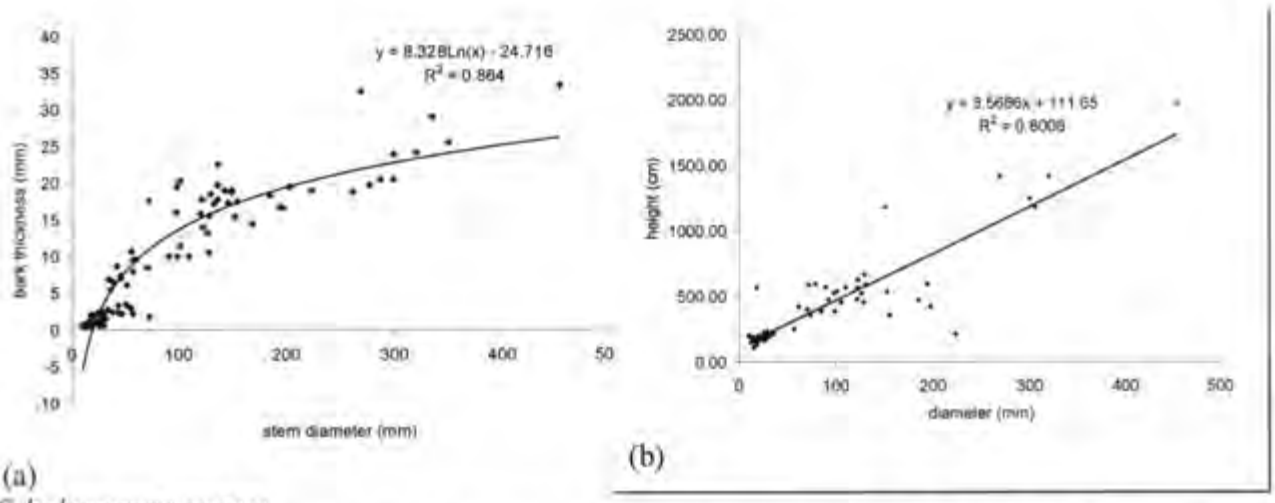
Looking at the overall growth patterns of the eight species as described by the linear, logistic or power function which best fitted the data, *A. nigrescens* is shown to have a weakly convex relationship between increasing stem diameter and investment in bark thickness (Fig. 2a). Although the allometric coefficient of 0.87 shows a negative allometry, the growth pattern is almost linear and there is no pronounced investment in bark thickness over increasing stem diameter. There is, however, a significant linear relationship between diameter and height ($R^2 = 0.75$, Fig. 2b) for *A. nigrescens*. This implies that there is not a marked initial investment in a thick stem or a rapid increase in height, but a continual investment in both. *Colophospermum mopane* initially invests in developing thick bark as it grows ($R^2 = 0.86$, Fig. 3a). Once it reaches a stem diameter of approximately 400 mm it no longer exhibits an increase in bark thickness. There is also a significant linear growth pattern between stem diameter and height ($R^2 = 0.80$, Fig. 3b) for this species, indicating that it invests in both equally.



(a) (b)

Acacia nigrescens

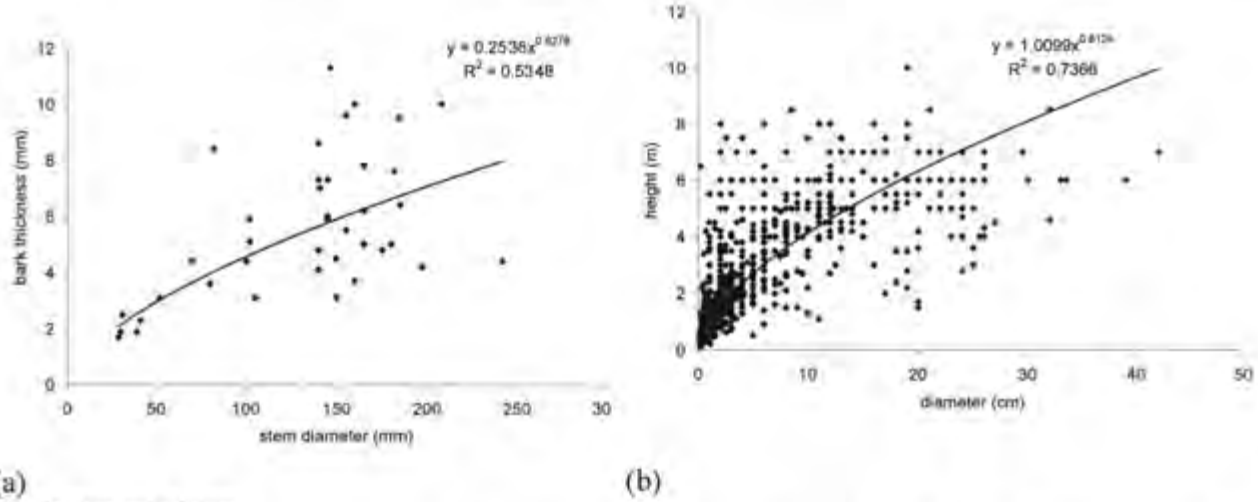
Fig. 2. (a) The relationship between stem diameter (mm) and bark thickness (mm) ($y = 0.14x^{0.87}$, $R^2 = 0.74$) and (b) the relationship between stem diameter (cm) and height (m) ($y = 0.23x + 0.41$, $R^2 = 0.75$) for *Acacia nigrescens*.



Colophospermum mopane

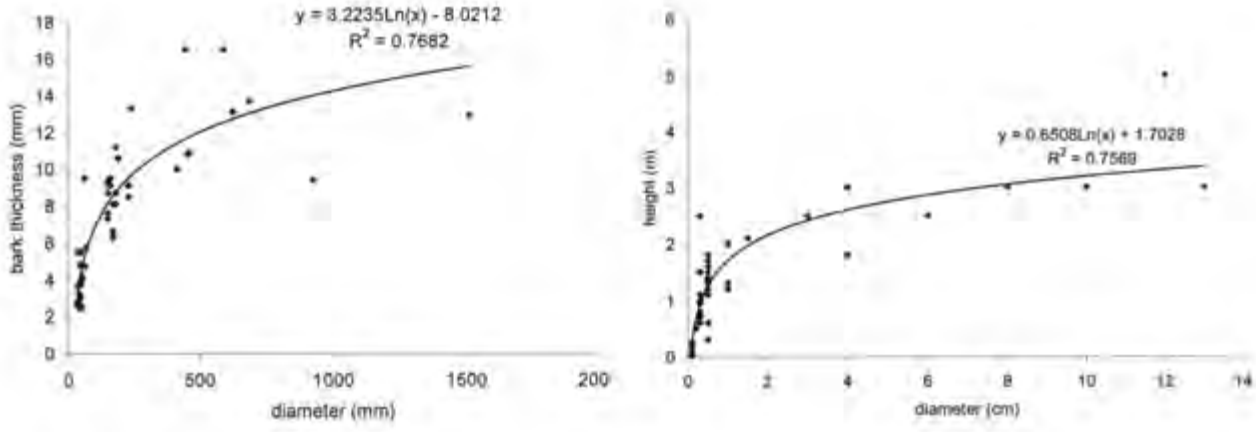
Fig. 3. (a) The relationship between stem diameter (mm) and bark thickness (mm) ($y = 8.33\text{Ln}(x) - 24.72$, $R^2 = 0.86$) and (b) the relationship between stem diameter (mm) and height (cm) ($y = 3.57x + 111.65$, $R^2 = 0.80$) for *Colophospermum mopane*.

Combretum apiculatum displays negative allometry, investing slightly more in its bark thickness ($y = 0.25x^{0.62}$, $R^2 = 0.53$, Fig. 4a) and in height ($y = 1.01x^{0.61}$, $R^2 = 0.74$, Fig. 4b) initially than in its stem diameter. *Combretum imberbe* also has a more pronounced initial investment in bark thickness ($y = 3.33\text{Ln}(x) - 8.02$, $R^2 = 0.77$, Fig. 5a) and in height ($y = 0.65\text{Ln}(x) + 1.70$, $R^2 = 0.76$, Fig. 5b) over growth in stem diameter. However after a diameter of approximately 10 cm is reached, most plants do not continue to increase bark thickness (Fig. 5a). This stem diameter corresponds with a mature height of approximately 3 m for *C. imberbe* (Fig. 5b).



Combretum apiculatum

Fig. 4. (a) The relationship between stem diameter (mm) and bark thickness (mm) ($y = 0.25x^{0.62}$, $R^2 = 0.53$) and (b) the relationship between stem diameter (mm) and height (m) ($y = 1.01x^{0.61}$, $R^2 = 0.74$) for *Combretum apiculatum*.

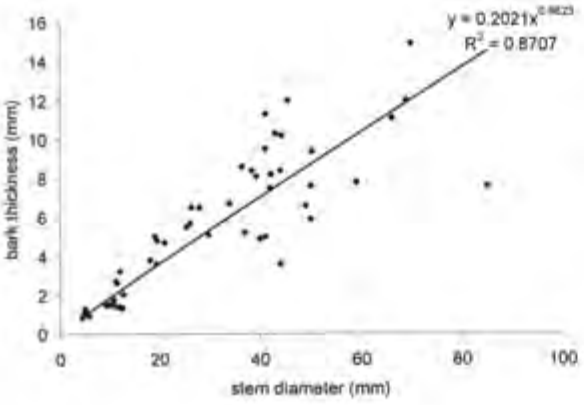


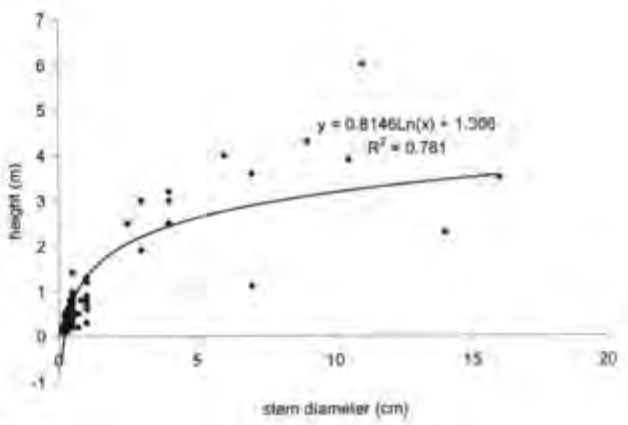
(a) (b)

Combretum imberbe

Fig. 5. (a) The relationship between stem diameter (mm) and bark thickness (mm) ($y = 3.22\text{Ln}(x) - 8.02$, $R^2 = 0.77$) and (b) the relationship between stem diameter (cm) and height (m) ($y = 0.65\text{Ln}(x) + 1.70$, $R^2 = 0.76$) for *Combretum imberbe*.

For *Dichrostachys cinerea* there is an almost isometric relationship between investment in bark thickness and stem diameter, with an allometric coefficient of 0.96 ($R^2 = 0.87$, Fig. 6a). There is a rapid initial increase in height with a thin stem (Fig. 6b) and it only develops a wider stem once it has reached a height of approximately 3 m. *Sclerocarya birrea, Terminalia sericea* and *Philenoptera violaceae* all show negative allometry with greater initial investments in bark thickness (Fig. 7a, 8a and 9a) compared to an increase in stem diameter. All three tree species show a decline in investment in bark thickness at a stem diameter of about 30cm. *Sclerocarya birrea* and *T. sericea* show negative allometry, investing in height rather than thicker stems (Fig. 7b and 8b), while *P. violacea* displays a linear growth relationship between height and stem diameter (Fig. 9b).

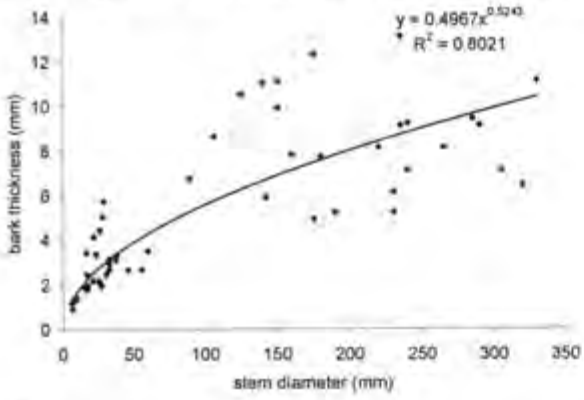


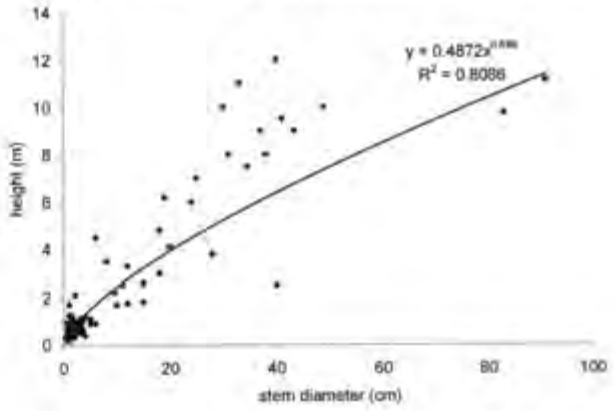


(a) (b)

Dichrostachys cinerea

Fig. 6. (a) The relationship between stem diameter (mm) and bark thickness (mm) ($y = 0.20x^{0.96}$, $R^2 = 0.87$) and (b) the relationship between stem diameter (cm) and height (m) ($y = 0.81\text{Ln}(x) + 1.31$, $R^2 = 0.78$) for *Dichrostachys cinerea*..

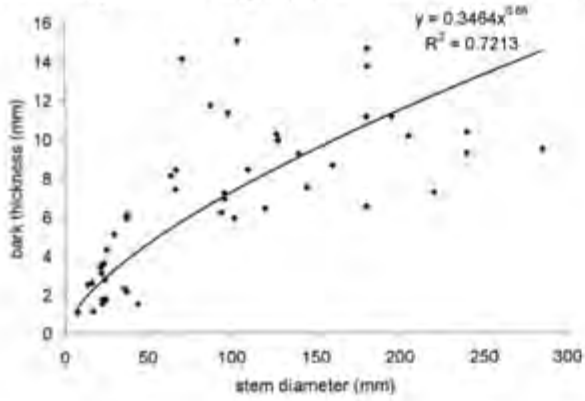


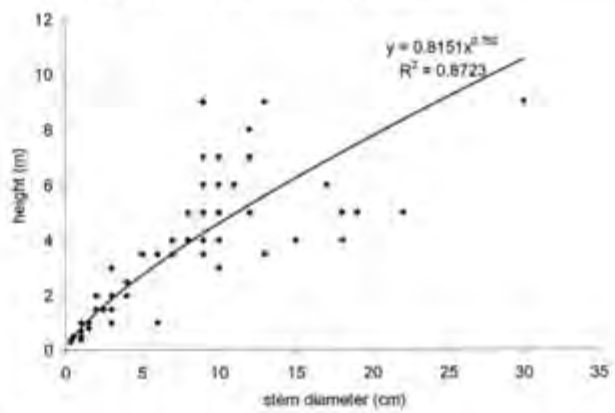


(a) (b)

Sclerocarya birrea

Fig. 7. (a) The relationship between stem diameter (mm) and bark thickness (mm) ($y = 0.49x^{0.52}$, $R^2 = 0.80$) and (b) the relationship between height (m) and stem diameter (cm) ($y = 0.49x^{0.69}$, $R^2 = 0.81$) for *Sclerocarya birrea*.

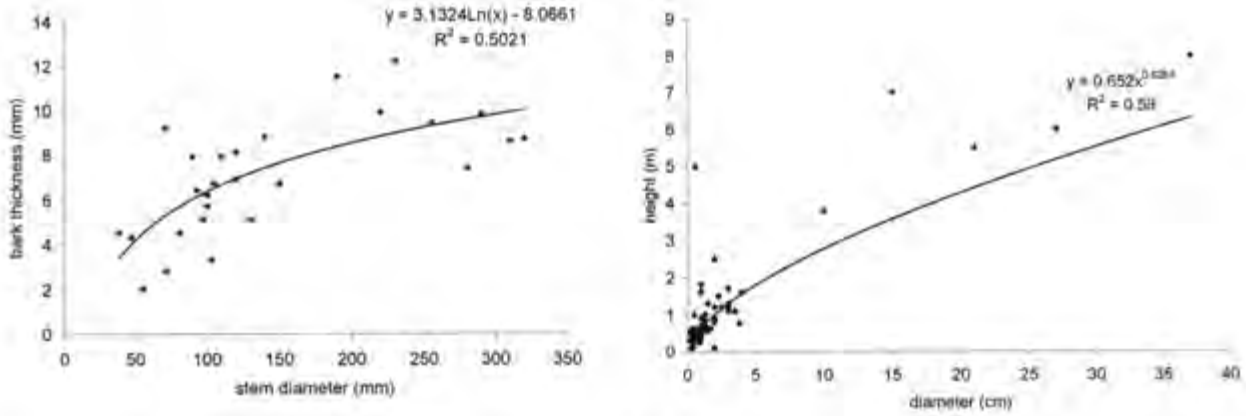




(a) (b)

Terminalia sericea

Fig. 8. (a) The relationship between stem diameter (mm) and bark thickness (mm) ($y = 0.35x^{0.66}$, $R^2 = 0.72$) and (b) the relationship between stem diameter (cm) and height (m) ($y = 0.82x^{0.75}$, $R^2 = 0.87$) for *Terminalia sericea*.



(a) (b)

Philenoptera violacea

Fig. 9. (a) The relationship between stem diameter (mm) and bark thickness (mm) ($y = 3.13\text{Ln}(x) - 8.06$, $R^2 = 0.50$) and (b) the relationship between stem diameter (cm) and height (m) ($y = 0.23x + 0.54$, $R^2 = 0.76$) for *Philenoptera violacea*.

Species specific topkill models

The plant species for which all three factors of plant height, fire intensity and season of burn had a significant effect on the topkill response were *Dichrostachys cinerea*, *Terminalia sericea* and *Philenoptera violaceae* (Table 2). For *Acacia nigrescens* ' topkill response is significantly affected by height and the product of fire intensity and season of burn (Table 2). For *Colophospermum mopane* and *Sclerocarya birrea* only height and season of burn are significant variables in explaining topkill (Table 2). Fire intensity was not a significant variable despite both species being exposed to fires with average intensities of 3100 kWm^{-1} (s.d. = 812 kWm^{-1}) and 2169 kWm^{-1} (s.d. = 1278 kWm^{-1}). These intensities are comparable to other species' intensities where fire intensity was a significant variable. For example *Combretum apiculatum* had a mean intensity of 2016 kWm^{-1} (s.d. = 954 kWm^{-1}), and this therefore indicates that this result is real and not due to chance. *Combretum apiculatum* and *C. imberbe* are not significantly affected by season of burn but by the height of the plants and by fire intensity.

Table 2. Species specific logistic models of topkill for *Acacia nigrescens, Colophospermum mopane, Combretum apiculatum, Combretum imberbe, Dichrostachys cinerea, Sclerocarya birrea, Terminalia sericea* and *Philenoptera violacea* in the experimental burn plots in Kruger National Park. (The data used for *Acacia nigrescens* were only from Trollope, the remaining species' topkill models were derived from data collected by both Trollope and UCT).

Species		Estimate	Std. error	p value	null deviance	residual deviance
Acacia nigrescens	Intercept	-7.71	10.38	0.45		
(n = 502)	Log(**height**)	-4.54	0.52	<2e-16	527.9	303.65
Skukuza + Satara	⊠ = 143.9 cm				(501 df)	(495 df)
	s.d. = ±100.3 cm					
	Sqrt(**Intensity**)	0.17	0.18	0.32		
	⊠ = 1900 kWm^{-1}					
	s.d. = ±1082 kWm^{-1}					
	Season (Feb)	15.83	10.69	0.13		
	Season (Oct)	15.32	10.47	0.14		
	Sqrt(**Inten**): **Season** (Feb)	-0.32	0.19	0.09		
	Sqrt(**Inten**): **Season** (Oct)	-0.25	0.18	0.15		
Colophospermum mopane	Intercept	5.19	0.70	1.66e-13		
(n = 1470)	Log(**height**)	-3.15	0.15	<2e-16	2466.7	1694.9
Mopane	⊠ = 192.1 cm				(2083 df)	(2077 df)
	s.d. = ±99.3 cm					
	Sqrt(**Intensity**)	-0.02	0.01	0.05		
	⊠ = 3100 kWm^{-1}					
	s.d. = ±812 kWm^{-1}					
	Season (Aug)	-1.25	0.35	0.0004		
	Season (Dec)	1.35	0.61	0.02		
	Season (Feb)	-2.63	0.38	1.35e-11		
	Season (Oct)	-0.96	0.34	0.005		
Combretum apiculatum	Intercept	0.95	1.28	0.46		
(n = 356)	Log(**height**)	-4.85	0.53	<2e-16	492.80	141.44
Skukuza + Satara	⊠ = 296.4 cm				(355 df)	(351 df)
	s.d. = ±227.7 cm					
	Sqrt(**Intensity**)	0.06	0.02	0.02		
	⊠ = 2016 kWm^{-1}					
	s.d. = ±954 kWm^{-1}					
	Season (Feb)	0.95	0.70	0.17		
	Season (Oct)	1.11	0.52	0.03		
Combretum imberbe	Intercept	-8.88	1752.97	0.9960		
(n = 138)	Log(**height**)	-3.01	0.62	1.28e-06	189.89	104.48
Satara + Skukuza	⊠ = 222.1 cm				(137 df)	(132 df)
	s.d. = ±152.6 cm					
	Sqrt(**Intensity**)	-0.09	0.03	0.01		
	⊠ = 2168 kWm^{-1}					
	s.d. = ±1185 kWm^{-1}					
	Season(Aug)	14.83	1752.96	0.99		
	Season(Feb)	14.07	1752.96	0.99		
	Season(Oct)	15.06	1752.96	0.99		
Dichrostachys cinerea	Intercept	-2.04	0.54	0.0001		
(n = 1454)	Log(**height**)	-4.13	0.24	<2e-16	1458.49	705.26
Pretoriuskop, Skukuza + Satara	⊠ = 129.5 cm				(1453 df)	(1449 df)
	s.d. = ±95.0 cm					
	Sqrt(**Intensity**)	0.08	0.009	<2e-16		
	⊠ = 2722 kWm^{-1}					
	s.d. = ±1601 kWm^{-1}					
	Season(Feb)	2.21	0.31	2.00e-12		
	Season(Oct)	1.57	0.32	1.21e-06		
Sclerocarya birrea	Intercept	-1.13	1.58	0.47		
(n = 176)	Log(**height**)	-2.59	0.36	1.63e-12	243.78	92.14
Pretoriuskop, Satara+Skukuza	⊠ = 285.76 cm				(175 df)	(171 df)
	s.d. = ±285.55 cm					
	Sqrt(**Intensity**)	0.02	0.02	0.35		
	⊠ = 2169 kWm^{-1}					
	s.d. = ±1278 kWm^{-1}					
	Season(Feb)	1.47	0.83	0.07		
	Season(Oct)	1.75	0.74	0.01		

Terminalia sericea (n = 2696) Pretoriuskop + Skukuza	Intercept	0.69	0.71	0.33		
	Log(**height**)	-4.07	0.25	<2e-16	1483.96 (1346 df)	493.03 (1342 df)
	☒ = 171.74 cm s.d. = ±182.44 cm					
	Sqrt(**Intensity**)	0.04	0.01	0.0005		
	☒ = 2381 kWm^{-1} s.d. = ±1456 kWm^{-1}					
	Season (Feb)	0.67	0.37	0.07		
	Season (Oct)	1.90	0.33	1.84e-08		
Philenoptera violacea (n = 104) Pretoriuskop, Satara + Skukuza	Intercept	-4.36	1.92	0.02		
	Log(**height**)	-3.44	0.75	5.67e-06	121.58 (103 df)	53.069 (99 df)
	☒ = 123.9 cm s.d. = ±189.1 cm					
	Sqrt(**Intensity**)	0.08	0.03	0.03		
	☒ = 2297 kWm^{-1} s.d. = ±1217 kWm^{-1}					
	Season(Feb)	2.96	1.16	0.01		
	Season(Oct)	1.36	0.96	0.15		

Bark thickness and bark moisture content

In the initial analysis *Colophospermum mopane* was included in the comparison of bark thickness to topkill probability. It was found to be an outlier however and the overall relationship between the individual species' bark thickness and corresponding probability of topkill was not significant ($R^2 = 0.12$, $F_{6,8} = 1.99$, $p = 0.20$, Fig. 10). When *C. mopane* was excluded a slightly higher amount of the variance in the probability of topkill response was explained by the species' bark thicknesses ($R^2 = 0.46$, $F_{1,5} = 6.14$, $p = 0.05$, Fig. 11), and it was significant at the 10% level. Data were not collected for *C. mopane*'s bark moisture content. The comparison of the other species' percentage bark moisture contents and probabilities of topkill showed a trend of the probability of topkill decreasing with higher bark moisture content (Fig. 11). The linear relationship between bark moisture content and the probability of topkill was only significant at the 10% level ($R^2 = 0.44$, $F_{5,7} = 6.48$, $p = 0.05$, Fig. 11). *Acacia nigrescens* has a low probability of topkill despite only having an intermediate value of bark moisture content compared to the other species (Fig. 12). *Acacia nigrescens* has the thickest bark of all the species analysed (Fig. 10 and 11) and so a combination of thick bark and bark moisture content may be important. Overall *C. apiculatum*, *C. imberbe* and *T. sericea* have thin bark, lower bark moisture content and show a correspondingly higher probability of topkill in comparison to the other species.

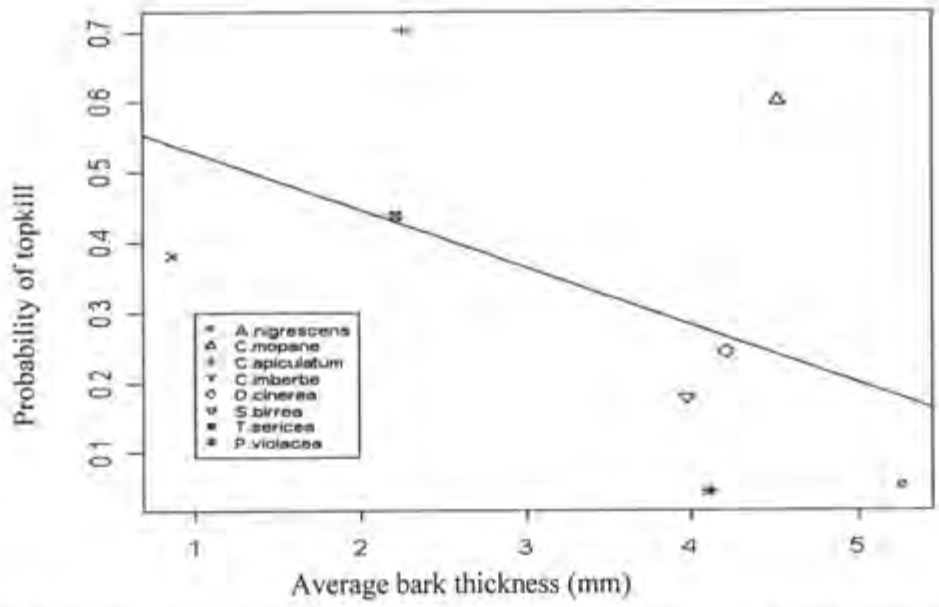


Fig. 10. Probability of topkill derived from species specific topkill models for 2m tall *Acacia nigrescens, Colophospermum mopane, Combretum apiculatum, Combretum imberbe, Dichrostachys cinerea, Sclerocarya birrea, Terminalia sericea* and *Philenoptera violacea* for a fire intensity of 2000 kWm^{-1} and an August burn. This is plotted against the average bark thickness (mm) of a 2m tall individual of each of the above species ($R^2 = 0.12$, $F_{6,8} = 1.99$, $p = 0.20$).

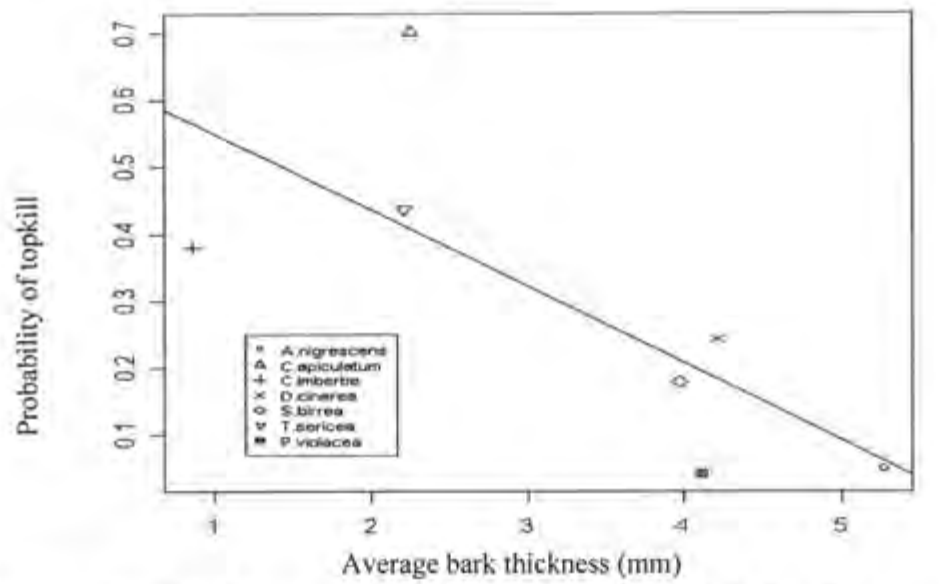


Fig. 11. Probability of topkill derived from species specific topkill models for 2m tall *Acacia nigrescens, Combretum apiculatum, Combretum imberbe, Dichrostachys cinerea, Sclerocarya birrea, Terminalia sericea* and *Philenoptera violacea* for a fire intensity of 2000 kWm^{-1} and an August burn. This is plotted against the average bark thickness (mm) of a 2m tall individual of each of the above species ($R^2 = 0.46$, $F_{1,5} = 6.14$, $p = 0.05$).

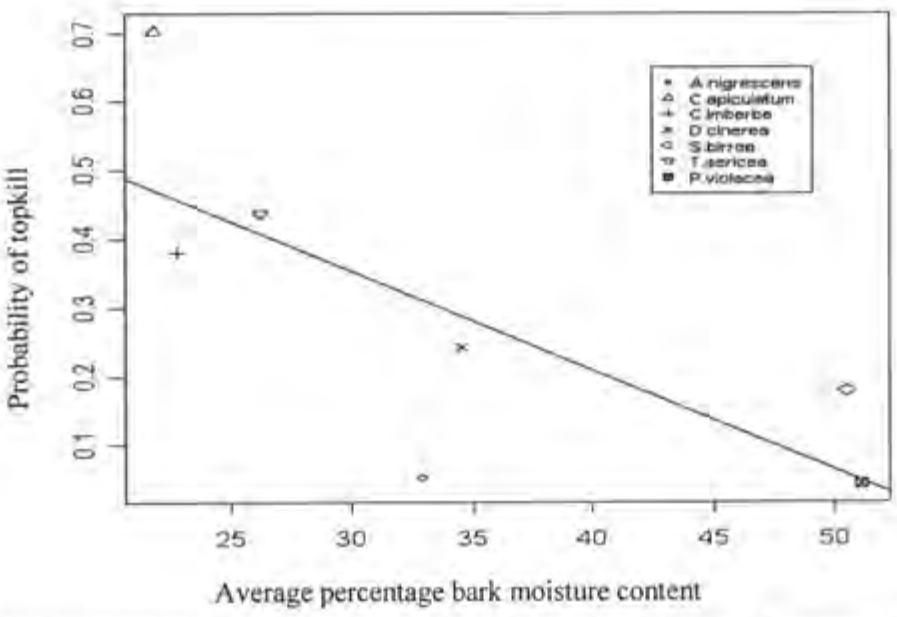
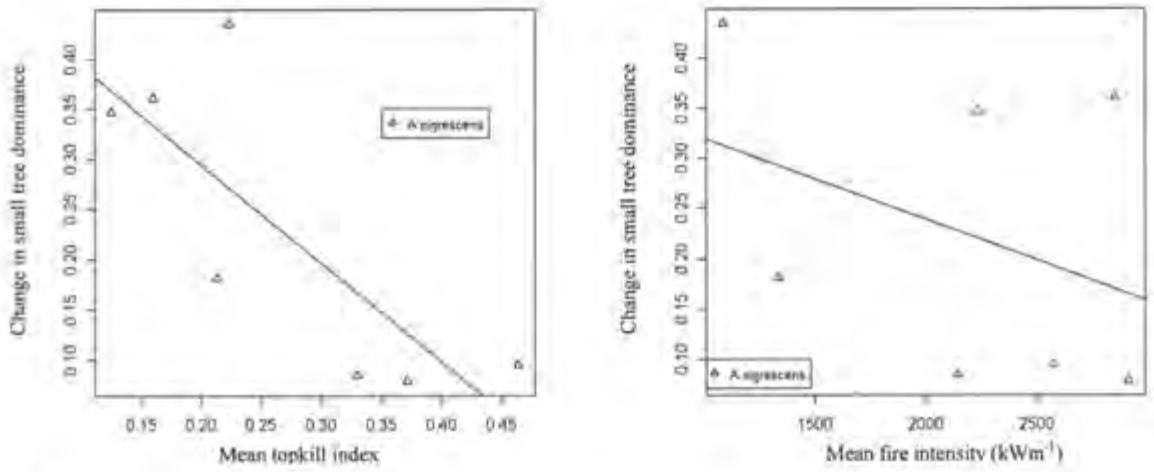


Fig. 12. Plot of percentage bark moisture content against the probability of topkill generated from the species specific topkill models for *Acacia nigrescens, Combretum apiculatum, Combretum imberbe, Dichrostachys cinerea, Sclerocarya birrea, Terminalia sericea* and *Philenoptera violacea*. The topkill model probabilities were generated for a 2m tall individual of each species exposed to a 2000 kWm^{-1} fire intensity and for an August burn. ($R^2 = 0.47$, $F_{5,7} = 6.48$, $p = 0.05$).

Predicting change in vegetation structure

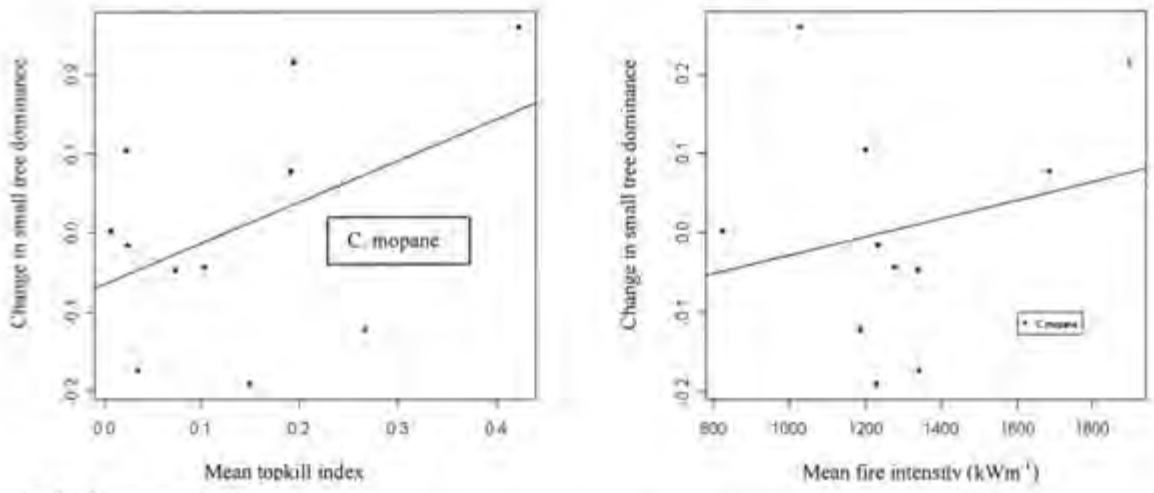
In *A. nigrescens, C. imberbe, D. cinerea, T. sericea* and *P. violacea* as the probability of trees not being topkilled by fire for three years increases the proportion of small trees in each burn plot between the two surveys increases (Fig. 13a, 15a, 16a, 17a and 18a). *Acacia nigrescens* and *T. sericea* are the only species which show a significant negative relationship between the topkill index and change in dominance ($R^2 = 0.56$, $p < 0.05$, Fig. 13a and $R^2 = 0.59$, $p < 0.05$, Fig. 17a respectively). *Colophospermum mopane* shows a trend of the proportion of small trees decreasing between the two surveys as the average probability of trees not being topkilled for three years in the respective burn plots increases (Fig. 14a). None of the species showed a significant linear relationship between the average fire intensity on each of the burn plots and the change in dominance of the size classes of trees between the two surveys (Fig. 13b, 14b, 15b, 16b, 17b and 18b). There were not enough trees for *Sclerocarya birrea* and *Combretum apiculatum* in many of the landscapes for this part of the analysis to be performed for these two species.



Acacia nigrescens

(a) **(b)**

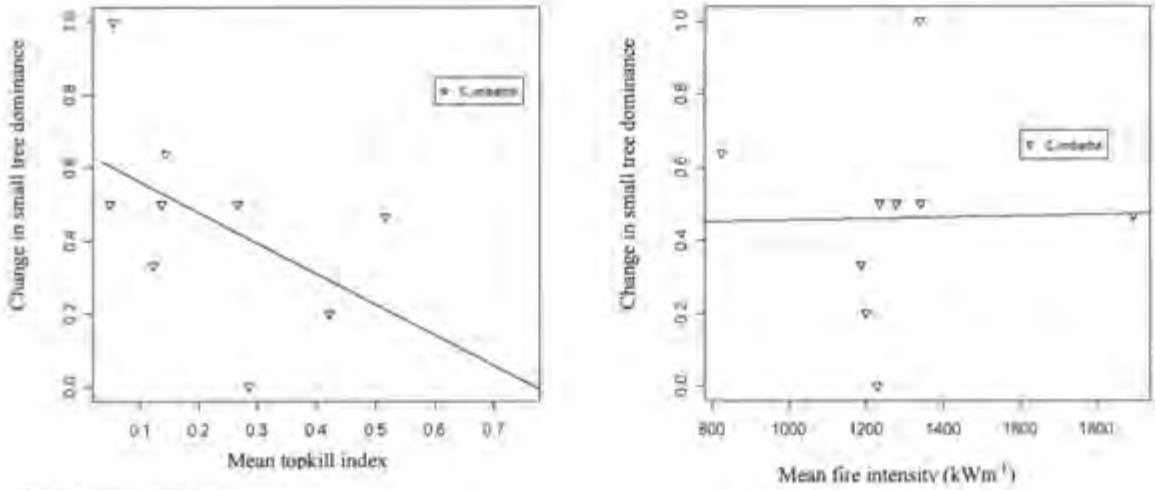
Fig. 13. (a) Plot of the change in small tree dominance (proportion of individual *Acacia nigrescens* less than 2 m tall out of the total number plants surveyed in 1996-99 subtracted from the proportion in 1956/7) against the topkill index of the mean probability of individual plants not experiencing topkill for three years on the different burn plots in the four landscapes in Kruger National Park ($R^2 = 0.56$, $F_{1,5} = 8.69$, $p = 0.03$). (b) Plot of the change in dominance against the average fire intensity of each burn plot ($R^2 = -0.024$, $F_{1,5} = 0.85$, $p = 0.39$).



Colophospermum mopane

(a) **(b)**

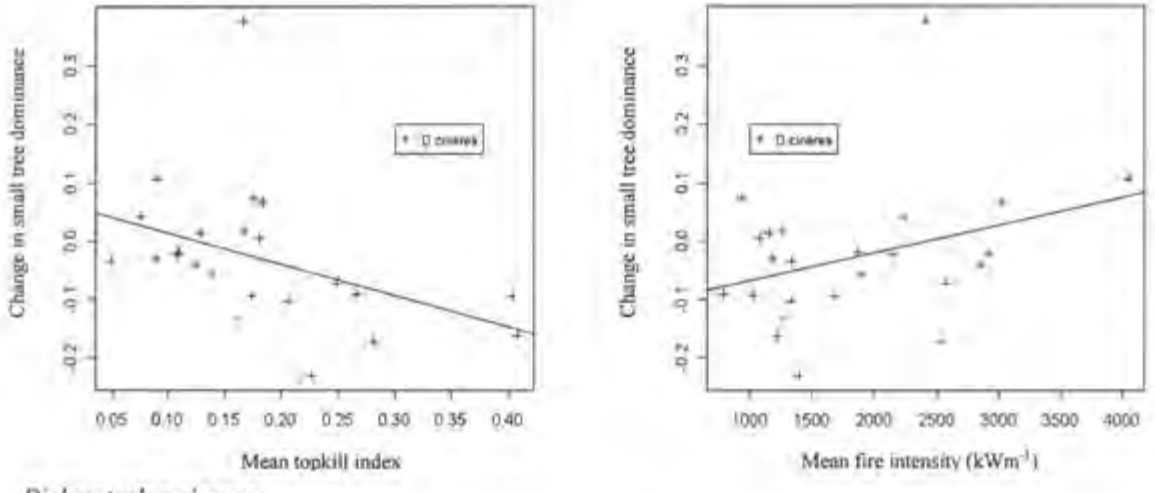
Fig. 14. (a) Plot of the change in small tree dominance (proportion of individual *Colophospermum mopane* less than 2 m tall out of the total number plants surveyed in 1996-99 subtracted from the proportion in 1956/7) against the topkill index of the mean probability of individual plants not experiencing topkill for three years on the different burn plots in the four landscapes in Kruger National Park ($R^2 = 0.11$, $F_{1,9} = 2.27$, $p = 0.16$). (b) Plot of the change in dominance against the average fire intensity of each burn plot ($R^2 = 0.05$, $F_{1,9} = 0.49$, $p = 0.49$).



Combretum imberbe

(a) **(b)**

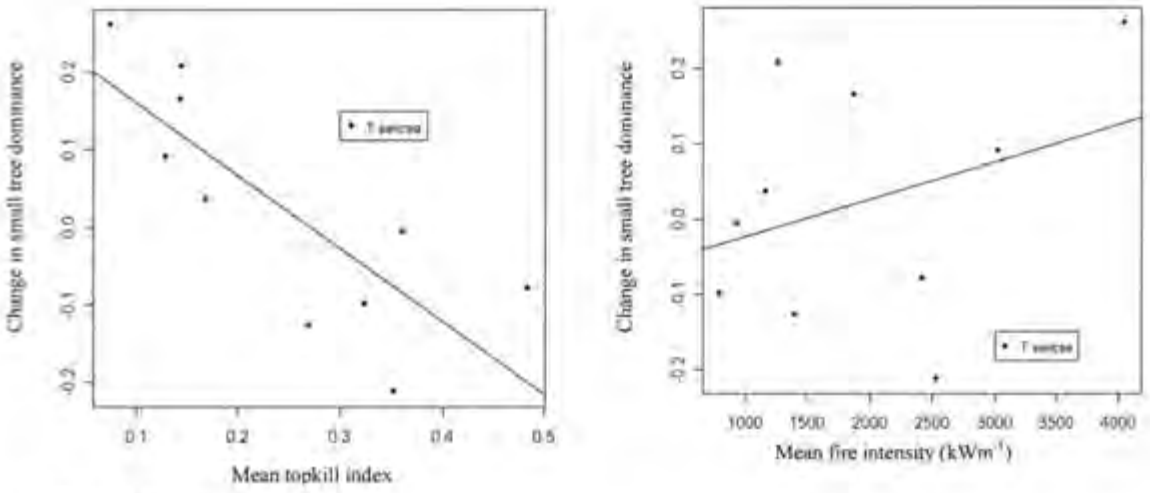
Fig. 15. (a) Plot of the change in small tree dominance (proportion of individual *Combretum imberbe* less than 2 m tall out of the total number plants surveyed in 1996-99 subtracted from the proportion in 1956/7) against the topkill index of the mean probability of individual plants not experiencing topkill for three years on the different burn plots in the four landscapes in Kruger National Park ($R^2 = 0.13$, $F_{1,7} = 2.24$, $p = 0.17$). (b) Plot of the change in dominance against the average fire intensity of each burn plot ($R^2 = -0.14$, $F_{1,7} = 0.002$, $p = 0.96$).



Dichrostachys cinerea

(a) **(b)**

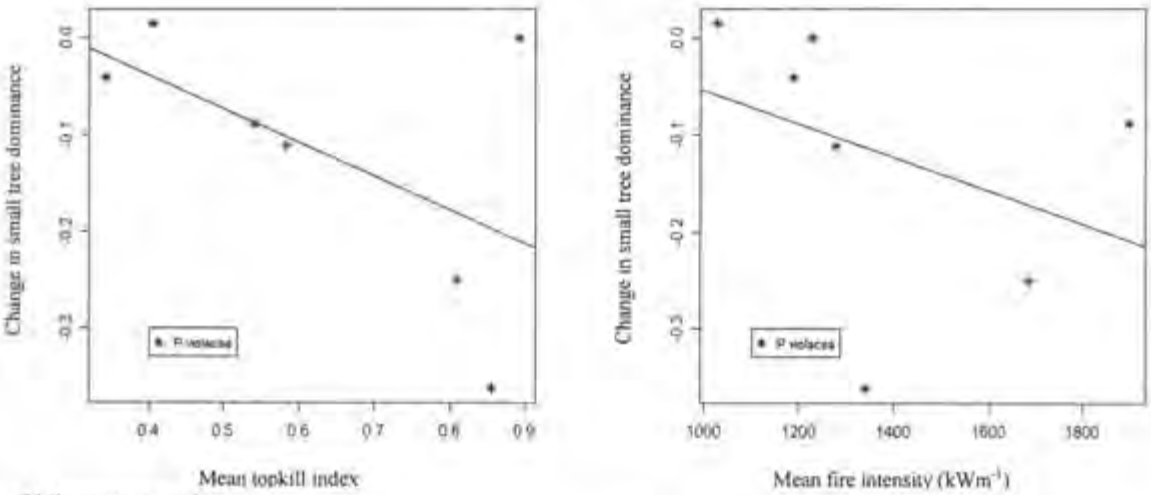
Fig. 16. (a) Plot of the change in small tree dominance (proportion of individual *Dichrostachys cinerea* less than 2 m tall out of the total number plants surveyed in 1996-99 subtracted from the proportion in 1956/7) against the topkill index of the mean probability of individual plants not experiencing topkill for three years on the different burn plots in the four landscapes in Kruger National Park ($R^2 = 0.13$, $F_{1,22} = 4.56$, $p = 0.04$). (b) Plot of the change in dominance against the average fire intensity of each burn plot ($R^2 = 0.07$, $F_{1,22} = 2.78$, $p = 0.10$).



Terminalia sericea

(a) **(b)**

Fig. 17. (a) Plot of the change in small tree dominance (proportion of individual *Terminalia sericea* less than 2 m tall out of the total number plants surveyed in 1996-99 subtracted from the proportion in 1956/7) against the topkill index of the mean probability of individual plants not experiencing topkill for three years on the different burn plots in the four landscapes in Kruger National Park ($R^2 = 0.59$, $F_{1,8} = 14.12$, $p = 0.005$). (b) Plot of the change in dominance against the average fire intensity of each burn plot ($R^2 = 0.001$, $F_{1,8} = 1.01$, $p = 0.34$).



Philenoptera violacea

(a) **(b)**

Fig. 18. (a) Plot of the change in small tree dominance (proportion of individual *Philenoptera violacea* less than 2 m tall out of the total number plants surveyed in 1996-99 subtracted from the proportion in 1956/7) against the topkill index of the mean probability of individual plants not experiencing topkill for three years on the different burn plots in the four landscapes in Kruger National Park ($R^2 = 0.17$, $F_{1,5} = 2.25$, $p = 0.19$). (b) Plot of the change in dominance against the average fire intensity of each burn plot ($R^2 = -0.02$, $F_{1,5} = 0.83$, $p = 0.40$).

Discussion

In this study I examined the role that fire plays in structuring the vegetation in the Kruger National Park. I investigated plant fire defence strategies by exploring the relationship between growth in bark thickness, tree height and stem diameter for eight dominant species in Kruger. With the exception of *D. cinerea,* all of the species show a trend of investing more in bark thickness than in stem diameter. *Dichrostachys cinerea* does not, however, attain a height that allows it to escape the fire trap. This suggests that bark thickness is related to topkill survival and that the other species are able to escape the fire trap as they develop thicker bark rather than investing in stem diameter. Investment in bark thickness is related to the type of bark plants have. *Combretum apiculatum* has been classified as having smooth bark, *Terminalia sericea* as having fissured bark and *Sclerocarya birrea* as scaly barked according to Nicolai (1989). He found that species with smooth or thin bark tend to invest less in developing bark than those with fissured or scaly bark.

Bark thickness has been shown to be positively correlated with increasing the protection of cambial tissue from being damaged by fire (Pinard and Huffman 1997). In a study by Uhl and Kauffman (1990) it was found that tree species with bark thicknesses below 3 mm were the least fire tolerant. *Terminalia sericea, Combretum apiculatum* and *Combretum imberbe* have higher probabilities of topkill associated with their bark thicknesses of less than 3 mm. It is noted however that bark moisture content is also important (Uhl and Kauffman 1990; Pinard and Huffman 1997). From this study bark moisture content does appear to play a role in reducing the probability of topkill and this should be explored further. Generally it was found that species that had thicker bark also have high bark moisture contents. Although *Acacia nigrescens* had thick bark, it only had an intermediate bark moisture content and this corresponded with a surprisingly low probability of topkill. Pinard and Huffman (1997) propose that other physical attributes of the bark such as its texture and the amount of fissuring are equally important. *Acacia nigrescens* has a thick, fissured bark and this might be an important factor in helping insulate the inner cambial tissue.

Assessing the factors that significantly affect the variance in topkill response it was found that plant height was a significant variable in all of the species. This lends support to the Gulliver hypothesis in that once plants reach a certain height they are immune to the effects of fire. As observed by Higgins *et al.* (2000) trees within the flame zone are most susceptible to fire, however those that are able to reach taller more fire-resistant size classes stand a better chance of surviving fires. Species with canopies high above the herbaceous layer are likely to experience less severe topkill (Bond and van Wilgen 1996). A future study looking at the relative growth rates of each of the species in this study between fires would be beneficial.

In terms of the other factors which influence topkill response, *Dichrostachys cinerea*, *Terminalia sericea* and *Philenoptera violacea* were found to have topkill responses affected by fire season and fire intensity. Trollope (1984) points out that fire intensity and season of burn are often closely related. In Kruger National Park fires in late winter and early summer at the end of the dry season, are often very intense, whereas fires in the wet season are usually much less intense. A hypothesis has been put forward that summer burning would constrain the population growth of *Dichrostachys cinerea* as at this stage in the plant's phenology carbon reserves are lowest after the initial spring flush and therefore post-burn re-growth would be stunted (Schutz 2003). Initial slow re-growth would affect the time taken to reach maturity and the size of the plant in the next burn, indirectly affecting fertility and mortality. This could also be true for the other species and should be explored further.

Sclerocarya birrea and *Colophospermum mopane* were shown to be unaffected by fire intensity. For *Colophospermum mopane* this could be due to the fact that the intensity of fires is strongly linked to combustion of its foliage which was not measured (E. February personal communication). The intensity values used are reliant on combustion of grass biomass and this may be an inappropriate measure for areas where *C. mopane* is found as the grass biomass in these areas is usually low. *Sclerocarya birrea* has thick bark and high bark moisture content and this may make it relatively immune to fire intensity. Trollope *et al.* (1995) found that the sensitivity of plant species in Kruger Park to fire

intensity was strongly linked to each species' bark thickness. Studies on *Sclerocarya birrea's* response to fire have shown that its vegetation response is more dependent on the effects of fire season and frequency than fire intensity (Jacobs and Biggs 2001). *Combretum imberbe* does not show a distinct pattern of being deciduous (Carr 1988) and this may be a possible reason why it is unaffected by fire season. *Combretum apiculatum* is deciduous, however, and one would have expected it to be more adversely affected by being burnt when it is investing in replacing the leaves in its canopy. Overall, the fact that not all of the species will be responsive to season of burn or fire intensity implies that managing the fire regime and the season of burn in Kruger National Park will not necessarily have the same effects on all of the species present.

This study then investigated how well topkill predicts observed changes in vegetation structure. It has been found that in general fire does not significantly affect the density of trees and shrubs, but rather the overall structure of woody vegetation (Jacobs and Biggs 2001). For most of the species in this study, the change in vegetation structure in relation to the probability of plants surviving fires may be explained by the plant species' abilities to escape the fire trap. Where there is a low average probability of a species not being topkilled only the plants which have gained a sufficient height to escape the fire trap will survive and there would therefore be a higher proportion of tall trees to small trees. Where there is a greater average probability of not being topkilled a greater number of smaller trees are found as they are able to persist in the fire trap. With *Colophospermum mopane*, the trees themselves can act as the fire trap as their leaves are highly flammable (E. February personal communication). In addition, low growth rates of *C. mopane* in low rainfall areas may hinder their ability to escape the fire trap (February *et al.* 2006). It is possibly only where the probability of topkill by fire is greatly reduced that taller trees can occur as they will then be able to grow tall. In a study by Kennedy and Potgieter (2003), it was found that height is one of the most significant aspects of *C. mopane's* morphology that is affected by fire. Where fire did not cause topkill *C. mopane* were found to be significantly taller than trees which were affected by fire (Kennedy and Potgieter 2003). In this study in Kruger however, other factors besides topkill response may be influencing the height structure of *C. mopane*.

From the results of this study fire does appear to play a significant role in structuring vegetation. The plant species studied exhibit adaptations such as developing thicker bark and growing above the fire trap which reduce the risk of topkill. For several of the species the topkill response can effectively predict the change in vegetation structure. The size structure of *Colophospermum mopane* appears to be affected by other factors besides fire, however, and future studies should investigate this further. Enslin *et al.* (2000) rightly note that fire should not be viewed as a single isolated factor influencing vegetation as other environmental influences such as climate, the degree of herbivory and soil types are also important in determining vegetation morphology and structure. Structural changes in savannas will potentially cause variation in microclimates and the distribution of resources such as nutrients and moisture (Ludwig *et al.* 2004 cited Higgins *et al.* submitted). This in turn will have an influence on biodiversity as specific species will be found in the different microclimatic conditions and different niches will be created. It is therefore important to try and understand the processes causing these structural changes so that they can be effectively managed.

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Appendix

Table 3. Parameter estimates of the different regression functions fitted to the stem diameter versus bark thickness and stem diameter versus height data for plant species in Kruger National Park.

Relationship	Species	Equation	R^2	Parameter	Estimate	Std. error	p-value	Null deviance	Residual deviance
Stem diameter versus bark thickness	*Acacia nigrescens*	y = a*x + c	R^2 = 0.69	c	2.03	0.69	<0.05	2171.94	22.16
				a	0.06	0.005	<0.05		
		y = c*x^a	R^2 = 0.74	c	0.14	0.51	<0.05	1086.96	11.21
				a	0.87	0.004	<0.05		
		y = a*Ln(x) – c	R^2 = 0.68	c	14.5	0.08	<0.05	1481.62	15.27
				a	5.36	0.0003	<0.05		
	Colophospermum mopane	y = a*x + c	R^2 = 0.81	c	1.38	0.56	0.02	1527.88	15.43
				a	0.08	0.004	<0.05		
		y = c*x^a	R^2 = 0.86	c	1.25	0.53	0.009	1392.01	14.20
				a	0.02	0.004	<0.05		
		y = a*Ln(x) – c	R^2 = 0.86	c	24.71	0.08	<0.05	2842.67	29.006
				a	8.32	0.0003	<0.05		
	Combretum apiculatum	y = a*x + c	R^2 = 0.3	c	2.22	0.07	<0.05	167.98	4.02
				a	0.02	0.0004	<0.05		
		y = c*x^a	R^2 = 0.53	c	0.25	0.88	0.01	167.04	4.51
				a	0.62	0.006	0.00004		
		y = a*Ln(x) – c	R^2 = 0.35	c	0.90	0.20	<0.05	177.96	4.80
				a	2.62	0.001	0.001		
	Combretum imberbe	y = a*x + c	R^2 = 0.45	c	5.57	0.54	<0.05	357.10	8.30
				a	0.009	0.001	<0.05		
		y = c*x^a	R^2 = 0.75	c	0.70	0.54	<0.05	348.90	8.30
				a	0.46	0.001	<0.05		
		y = a*Ln(x) – c	R^2 = 0.76	c	8.02	0.07	<0.05	426.60	10.15
				a	3.22	0.0001	<0.05		
	Dichrostachys cinerea	y = a*x + c	R^2 = 0.72	c	0.82	0.49	0.09	180.11	3.60
				a	0.15	0.01	<0.05		
		y = c*x^a	R^2 = 0.87	c	0.20	0.48	0.08	180.12	3.60
				a	0.96	0.01	<0.05		
		y = a*Ln(x) – c	R^2 = 0.74	c	6.82	0.12	<0.05	272.52	5.45
				a	3.91	0.002	<0.05		
	Sclerocarya birrea	y = a*x + c	R^2 = 0.58	c	2.58	0.51	<0.05	325.61	6.26
				a	0.02	0.003	<0.05		
		y = c*x^a	R^2 = 0.80	c	0.49	0.44	<0.05	242.43	4.84
				a	0.52	0.002	<0.05		
		y = a*Ln(x) – c	R^2 = 0.68	c	2.30	0.11	<0.05	292.65	5.85
				a	4.09	0.0005	<0.05		
	Terminalia sericea	y = a*x + c	R^2 = 0.50	c	3.14	0.84	<0.05	762.66	14.6
				a	0.03	0.006	0.001		
		y = c*x^a	R^2 = 0.72	c	0.34	0.62	<0.05	384.55	8.01
				a	0.66	0.005	<0.05		
		y = a*Ln(x) – c	R^2 = 0.64	c	3.24	0.12	<0.05	460.40	9.59
				a	6.73	0.0007	<0.05		
	Philenoptera violacea	y = a*x + c	R^2 = 0.43	c	4.11	0.76	<0.05	97.31	3.89
				a	0.02	0.004	0.0001		
		y = c*x^a	R^2 = 0.47	c	0.55	0.73	<0.05	97.31	3.89
				a	0.51	0.004	<0.05		
		y = a*Ln(x) – c	R^2 = 0.50	c	8.06	0.11	<0.05	104.53	4.18
				a	3.13	0.0005	0.00003		
Stem diameter versus height	*Acacia nigrescens*	y = a*x + c	R^2 = 0.75	c	0.41	0.28	0.31	873.10	5.74
				a	0.22	0.15	<0.05		
		y = c*x^a	R^2 = 0.57	c	0.62	0.28	0.31	873.10	5.74
				a	0.53	0.15	<0.05		
		y = a*Ln(x) + c	R^2 = 0.48	c	0.78	0.09	<0.05	1275.08	8.38
				a	0.74	0.02	<0.05		
	Colophospermum mopane	y = a*x + c	R^2 = 0.80	c	111.64	26.57	<0.05	1726141	25763.29
				a	3.56	0.21	<0.05		
		y = c*x^a	R^2 = 0.78	c	29.87	26.18	<0.05	1726141	25763.29
				a	0.60	0.21	<0.05		
		y = a*Ln(x) – c	R^2 = 0.61	c	688.04	0.07	<0.05	1994966	29775.61
				a	279.4	0.0002	<0.05		
	Combretum apiculatum	y = a*x + c	R^2 = 0.56	c	1.19	0.18	<0.05	18933.87	16.78
				a	0.23	0.06	<0.05		
		y = c*x^a	R^2 = 0.73	c	1.00	0.18	<0.05	18933.87	16.78

			a	0.61	0.06	<0.05		
	y = a*Ln(x) + c	R^2 = 0.66	c	1.39	0.05	<0.05	22770.51	20.18
			a	1.26	0.009	<0.05		
Combretum imberbe	y = a*x + c	R^2 = 0.65	c	0.95	0.41	<0.05	158.91	2.99
			a	0.25	0.25	<0.05		
	y = c*x^a	R^2 = 0.53	c	1.37	0.41	<0.05	158.91	2.99
			a	0.53	0.25	<0.05		
	y = a*Ln(x) + c	R^2 = 0.75	c	1.70	0.24	<0.05	192.07	3.62
			a	0.65	0.06	<0.05		
Dichrostachys cinerea	y = a*x + c	R^2 = 0.68	c	0.28	0.07	<0.05	284.21	1.07
			a	0.33	0.08	<0.05		
	y = c*x^a	R^2 = 0.67	c	0.78	0.02	<0.05	47.69	0.18
			a	0.90	0.01	<0.05		
	y = a*Ln(x) + c	R^2 = 0.78	c	1.30	0.06	<0.05	87.37	0.33
			a	0.81	0.007	<0.05		
Sclerocarya birrea	y = a*x + c	R^2 = 0.79	c	0.63	0.94	0.23	5600.24	57.73
			a	0.16	0.25	<0.05		
	y = c*x^a	R^2 = 0.80	c	0.48	0.15	0.00004	188.92	1.94
			a	0.69	0.008	<0.05		
	y = a*Ln(x) + c	R^2 = 0.70	c	0.19	0.11	0.000001	436.47	4.49
			a	1.75	0.001	<0.05		
Terminalia sericea	y = a*x + c	R^2 = 0.60	c	1.25	0.80	0.50	1027.53	14.67
			a	0.31	0.18	<0.05		
	y = c*x^a	R^2 = 0.87	c	0.81	0.28	0.00001	166.95	2.38
			a	0.75	0.02	<0.05		
	y = a*Ln(x) + c	R^2 = 0.69	c	0.90	0.09	<0.05	234.15	3.34
			a	1.75	0.006	<0.05		
Philenoptera violacea	y = a*x + c	R^2 = 0.76	c	0.54	0.43	0.005	606.06	8.53
			a	0.22	0.22	<0.05		
	y = c*x^a	R^2 = 0.58	c	0.65	0.09	<0.05	39.77	0.56
			a	0.62	0.01	<0.05		
	y = a*Ln(x) + c	R^2 = 0.55	c	0.98	0.11	0.57	66.00	0.94
			a	1.05	0.004	<0.05		