Which traits determine shifts in the abundance of tree species in a fire prone savanna?

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Summary

1. Fire is a process that shapes the structure and composition of vegetation in many regions. Species in these regions have presumably evolved life-history strategies that allow success in fire-prone environments.

2. In this study we examine the extent to which the ecological success of savanna trees is determined by traits that enhance the capacity to tolerate fire and or traits indicative of an ecophysiological capacity for rapid growth. We define ecological success as the relative change in stem density over the course of a long term (circa 40 year) fire experiment conducted in the Kruger National Park, South Africa.

3. We first examine the extent to which differences in fire susceptibility can be explained by allometries describing bark properties and tree size. We then examine whether these differences in fire tolerance can explain observed shifts in abundance.

4. We show that species differ in their topkill responses (probability of above ground mortality) and that these differences are explained in part by differences in bark moisture content and the allometry between height and diameter. Contrary to previous studies we find no evidence that bark thickness is important in explaining susceptibility to topkill.

5. Synthesis. Fire tolerance traits did explain a significant component of the variance in observed shifts in the abundance of tree species. However, traits related to the carbon economy of photosynthesis were also important.

Keywords: Fire, savanna, topkill, growth, plant functional traits, shifts in abundance

Introduction

Fire is a process that shapes the structure of savannas. Empirical and modelling studies have shown that fire causes the biomass of savanna regions to deviate strongly from its climate potential (Bond et al. 2005, Higgins et al. 2010). Yet population level studies have shown that population size can, in savannas, be resilient to fire (Higgins et al. 2000). The apparent paradox between demographic resilience and structural responsiveness can be resolved by invoking the concept of topkill (Higgins et al. 2007, Prior et al. 2010).

Topkill can be defined as the partial or total mortality of above ground biomass. Plants respond to topkill injury by resprouting either epicormically, basally or by root-suckering. Epicormic resprouting is possible when the bark is thick enough to protect the buds, while resprouting from below-ground organs or buds is possible because the soil insulates the below-ground parts from heat (Whelan 1995, Bond and van Wilgen 1996). Although topkill is a set-back to plants that causes them to regress in structural stage, fire damage in savannas is seldom enough to cause whole-plant mortality (Bond and van Wilgen 1996, Hoffmann et al. 2009, Werner and Franklin 2010). Experimental studies have shown that several repeated events in which above ground biomass are removed are required to induce plant mortality in fire prone environments (Zedler et al. 1983, Bond and van Wilgen 1996, Schultz et al. 2009).

Repeated topkill inducing fires, even when they do not cause mortality, have the potential to prevent trees from progressing to larger size classes. This phenomenon has been dubbed the Gulliver syndrome, which draws attention to the potential of suppressed individuals to be giants should they escape the topkill cycle (Bond and van Wilgen 1996). Silvertown (1982) dubbed this phenomenon the Oskar syndrome, drawing attention to the potentially advanced age of the suppressed individuals. Important in both concepts is that the suppressed individuals are not reproductive. Hence, even without fire induced mortality of whole plants, repeated topkill could in theory prevent the recruitment of reproductive individuals which would eventually lead to local extinction (Higgins et al. 2000).

Topkill occurs when stems are exposed to critical temperatures for a sufficient length of time (Levitt 1972, Michaletz and Johnson 2007). The exact nature of the physiological damage of fire is not clear (Midgley et al. 2010). Many authors argue that cambial damage is what causes stem mortality, and much of the empirical work focuses on cambial cell mortality (Dickinson and Johnson 2004). Damage to the cambium can result in topkill through two pathways. First, if the cambium and phloem surrounding the entire circumference of the stem is killed (girdling), the photosynthate cannot be transported from the leaves to the roots. Second, if all epicormic buds within the canopy are killed, no new post-fire growth can occur. However, Balfour and Midgley (2006) and Moncrieff et al. (2008) illustrate that cambial death is not primarily responsible for topkill and some authors (Midgley et al. 2010, Kavanagh et al. 2010) argue that the rapid nature of topkill is more consistent with the catastrophic failure of xylem transport, rather than the slow death by starvation that would be associated with cambial damage.

Independent of whether the physiological cause of topkill is xylem failure or cambial damage, it is widely accepted that height can elevate the more fire sensitive canopies beyond the reach of flames and that bark can protect exposed stems from critical temperatures (e.g. Vine 1968, Gill and Ashton 1968, Bauer et al. 2010). There seems to be confusion in the literature as to whether moisture in the bark protects stems from fire damage. Bark moisture may be a double edged sword. The high conductivity of water ensures that moisture in the bark facilitates the transfer of heat into the stem (Michaletz and Johnson 2007, Midgley et al. 2010), while the high specific heat capacity of water means that it can prevent the bark from igniting (Gill and Ashton 1968). The question of which of these two counteracting effects dominates is addressed by Jones et al. (2004) who use a one-dimensional stem heating model that considers how the thermal properties of bark and wood are influenced by moisture and temperature. This analysis suggests that high bark moisture contents can protect stems from critical temperatures.

The probability that a stem suffers topkill in a fire is additionally influenced by fire intensity (Ansley et al. 1998, Williams et al. 1999) and by the plant's metabolic phase. It is, for instance, known that metabolically inactive tissue can be exposed to higher temperatures without damage (Levitt 1972). Similarly the heat-induced xylem embolisms proposed by Midgley et al. (2010) are more likely during metabolically active periods when the water column within xylem conduits is under higher tension and more unlikely in fires that occur during the dry season when many savanna tree species have lost their leaves.

The previous paragraphs suggest that fire intensity, tree height, bark thickness, bark moisture and metabolic phase could interact to influence the probability of topkill and that topkill probabilities should influence the structure and abundance patterns of tree species in savannas. Gignoux et al. (1997) however draw attention to the fact that investment in structural defence against fire is not the only strategy for success in fire prone environments. One alternative strategy is to invest in rapid growth in an attempt to attain a stem size that is insensitive to fire (Gignoux et al. 1997). In this view, an optimal life history strategy is simply to grow faster than competitors, thus increasing resource capture and the chance of attaining a fire resistant size. This view implies that traits indicative of rapid growth might be characteristic of successful savanna tree species.

The aims of this study are (1) to elucidate the effect of fire season, tree size and fire intensity on the probability of topkill; (2) explore whether species differ in their topkill responses; (3) explore whether allometries between diameter and height, bark-thickness and bark moisture content can explain between-species variance in topkill response; (4) examine whether topkill or ecophysiological indicators of growth can explain long-term changes in tree densities in a semi-arid African savanna.

Methods

Study site and experimental burn plots

The Kruger National Park (KNP) is located in the savanna biome of South Africa. The data we analyse are primarily derived from an on going fire experiment that was initiated in 1954. The experimental burn trials are repeated in four representative landscapes of the Kruger National Park. The Mopani landscapes are dominated by *Colophospermum mopane* growing on Basalt derived soils, mean annual precipitation (MAP) is 447 mm. The Satara landscapes are dominated by *Acacia nigrescens* growing on Basalt derived soils, MAP is 537 mm. The Skukuza landscapes are dominated by *Combretum* species on granite soils, MAP is 550 mm. The Pretoriuskop landscapes are dominated by *Terminalia sericea* growing on granite soils, MAP is 737 mm.

Within each landscape the experiment is replicated four times. Each replicate consists of twelve different experimental treatments and each treatment is implemented in a seven hectare plot. Eleven treatments manipulate the season and frequency of burning, while a twelfth treatment excludes fire. The eleven burning treatments are April (late growing season) biennial and triennial; August (dry season) annual, biennial and triennial; October (late dry season) biennial and triennial; December (early growing season) biennial and triennial; February (growing season) biennial and triennial. Biggs et al. (2003) provide more information on the experiment and its design and Gertenbach (1983) provides a detailed description of the landscapes included in this study.

Species names follow Palgrave (1983). For figures we plot abbreviations of the species names (species names and abbreviations are listed in supplementary Table 1).

Topkill data

Forty three experimental burn plots that were scheduled to burn during the sampling period were used for this analysis. On each of these plots the intensities of head fires were measured during the routine application of the experimental fires using the method described by Trollope and Potgieter (1985). This method is based on Byram's (1959) concept of fire line intensity, which describes fire intensity as the product of fuel consumed, heat yield of fuel and the rate of fire spread.

Each plot has approximate dimensions of 350 x 200 m. Plants within 20 m of the plot boundary were excluded from the survey. In an initial survey conducted on the Satara, Skukuza and Pretoriuskop plots the closest individual to 20 evenly spaced points along two 300 m long transects was sampled. The species, size (height was used to index size), whether the individual was topkilled (topkill was defined as a 100% reduction in tree height caused by the fire), and whether the individual had resprouted were recorded. To ensure enough time for recovery after fire, resprouting was evaluated in the growing season following the fire. In a subsequent survey, in the Mopani landscape, only individuals of *Colophospermum mopane* (the Mopani landscape is essentially mono-dominant) were sampled; and the sampling was stratified to ensure an even spread of individuals in different size classes.

In the data most individuals suffered either a 100% reduction in height or only slight reductions (<15%). For this reason we choose to model topkill as a binary response (topkilled or not-topkilled ($y = \{1; 0\}$)). The probability p of topkill was analysed using a logistic regression model,

$$
\begin{aligned}
y &\sim bern(p) \\
\mathrm{logit}(p) &= \beta_0[S] + \beta_1[S]\log(H) + \beta_2[S]\sqrt{I} + \beta_3[S]M.
\end{aligned}
$$

Here the β parameters are the regression coefficients describing the effects of height (H), fire intensity (I) and fire season (M) on topkill. Fire season refers to the month in which a fire was applied (August, October, December, February), which we simplified into dry (August, October) or wet season (December, February, April) fires. The β coefficients are assumed to vary with species S. We included all species in the analysis that had more than 20 individuals sampled (38 species); 8684 individuals were included in the analysis. The parameters were estimated using Bayesian methods. The β parameters were assumed to have normal, uninformed priors (mean = 0, variance 1000). The variance of these priors were assumed to be from uninformed uniform distributions (range = 0 - 10). We used JAGS (Plummer 2010) to estimate the parameters using MCMC sampling. The output from JAGS was analysed in R (R Development Core Team 2009) using the coda package (Plummer et al. 2009).

Plant functional traits

We collected, for common species in the topkill data set, allometric data on plant functional traits (see table S2 for a list of the species included in these analyses). We recorded tree size (height and diameter), bark thickness, bark moisture content, wood density and specific leaf area. These data were collected in the KNP, but not necessarily in the experimental burn plots. We selected 25 individuals of each species that appeared not to be damaged by large herbivores (elephant damage is common in the KNP) and that were single stemmed. Diameter was derived from the circumference measured above the basal swelling, but below any branching of the stem. Tree height was measured using a ranging rod for smaller trees and a Clinometer for larger trees. Bark thickness was measured using a vernier scale at the thickest and thinnest portion of each of two bark samples removed from the main stem of each individual (the mean of these four measurements was used as the estimate of bark thickness for an individual; estimates were obtained for individuals of different sizes). These bark samples were wet weighed, dried and reweighed, yielding estimates of bark moisture content. Two wood samples were removed from each individual and the volume displacement method (Chave 2006) was used to estimate density of the wood samples. For specific leaf area we sampled 5 leaves per individual, these were scanned using a LI-3000C leaf area meter and subsequently weighed. Leaves were selected following guidelines provided by Cornelissen et al. (2003).

We determined the C and N concentrations as well as the isotopic ratios 15N/14N and 13C/12C in the leaf samples using a Thermo Finnigan Delta plus XP Mass Spectrometer and Thermo Finnigan Flash EA1112 Elemental Analyser with automatic sampler (Thermo Electron Corporation, Milan, Italy). Our own internal standards were run to correct for drift in our reference gas and to calibrate the results relative to atmospheric N_2 for N and Pee Dee Belemnite for C. Deviations from the standard are denoted by the term δ for both 15N/14N as well as 13C/12C ratios and the results expressed as parts per thousand (‰). Precision of duplicate analysis was 0.1‰ for carbon and 0.2‰ for nitrogen.

In total 25 individuals were sampled for each of 14 species. The leaves of 5 of the 25 individuals sampled for each species were analysed for C, N, δ^{13}C and δ^{15}N. The log of response variables described in the previous paragraphs (y) were regressed against stem diameter (D) using the model,

$$
\begin{aligned}
y &\sim \text{normal}(\mu, \sigma) \\
\mu &= \beta_0[S] + \beta_1[S] \log(D).
\end{aligned}
$$

Here the β parameters are the regression coefficients, which are assumed to vary with species S. The parameters were estimated using Bayesian methods. These parameters were assumed to have normal, uninformed priors (mean 0). The variance of these priors were assumed to be from uninformed uniform distributions (range 0 - 20). The variance σ was also assumed to have an uninformed uniform prior (mean 0, variance 10). We used JAGS (Plummer 2010) to estimate the parameters using MCMC sampling. The output from JAGS was analysed in R (R Development Core Team 2009) using the coda package (Plummer et al. 2009).

Photosynthetic capacity

For photosynthetic capacity we used a Licor 6400 to derive A-Ci curves (curves of the response of photosynthetic rate to changes in leaf internal CO_2 concentration) following the field protocol used by Xu and Baldocchi (2003). This protocol involves allowing the leaf to acclimatise for 30 minutes to a high (1000 ppm) chamber CO_2 concentration and then programing a decrease in CO_2 concentration in the sequence 1000, 700, 500, 360, 200, 150, 100, 50 ppm. The leaves were given eight minutes to acclimatise to each CO_2 level before measuring the gas exchange parameters. Light intensity was set to 800 μmol.m^2.s^{-1}. We used the A-Ci curves to estimate several key parameters of the Farquhar et al. (1980) model of photosynthesis (maximum rate of Rubisco carboxylation V_{cmax}, maximal electron transport rate J_{max}, mitochondrial respiration in light R, CO_2 photo-compensation point Γ^*, conductance for CO_2 diffusion from inter-cellular airspace to the site of carboxylation g_m; the notation follows Patrick et al. 2009). We used a hierarchical Bayesian method for estimating the parameters (Patrick et al. 2009). This method provides several advantages over earlier methods. First, there is no need to subjectively prescribe the internal CO_2 concentration at which photosynthesis is carboxylation versus electron transport limited. Second it allows g_m to be estimated; some protocols for estimating V_{cmax} from A-Ci curves assume that g_m is a constant and this assumption can bias estimates of V_{cmax} and J_{max}(von Caemmerer 2000, Sharkey et al. 2007). Third, it allows species level parameter estimates to be informed by estimates derived across species. Finally, it allows us to use prior information on parameter values to inform parameter estimates. Patrick et al. (2009) present two options for estimating the temperature dependencies of the photosynthetic parameters; we use their peaked temperature dependence functions. Our implementation closely follows Patrick et al.'s (2009) code.

Change in tree densities

We analysed data emerging from two woody vegetation surveys conducted on the experimental burn plots, the first was conducted in 1956/57 and the second between 1996 and 1999 (Higgins et al. 2007). The later survey replicated the methods used in the original survey. The surveys recorded the size-class, and species of each woody individual encountered on two belt transects on each experimental plot. The belt transects were orientated to run from corner to corner of each plot. In the initial survey, each belt transect was 305 x 1.52 m in size, in the second survey the transect width was increased to 2 m, and the transect length varied from 150 to 500 m. The shorter transect lengths are due to the splitting of two plots in each block in 1979 to create additional treatments (data from these additional treatments are not analysed here). In all cases, transect dimensions are known and are used to express the data as densities. The data from the transect pairs were pooled prior to analysis. We use these data to estimate the change in density of 41 common species (species with at least 25 individuals on a plot in the initial survey) between the two survey periods. As described in the section *Study site and experimental burn plots*, there were 12 fire treatments in this experiment, and each treatment was replicated 4 times in each of 4 landscapes, yielding a total of were 192 plots. For this study we exclude the fire exclusion plots (leaving 176 plots) . The response variables (y) we consider are changes in tree density (ratio of density at time 2 to density at time 1), the log of the change in density of large trees (ratio density of >2m tall trees at time 2 to density of >2m tall trees at time 1) and the change in the proportion of large trees (ratio proportion of individuals > 2 m at time 2 to proportion of individuals > 2m at time 1). These data were analysed using linear mixed models using the following structure,

$$y \sim TRAITS + LANDSCAPE + FRI + SEASON + 1|SPECIES,$$

where y is one of the response variables, $TRAITS$ is a shorthand for parameters derived from the models described in the sections sections *topkill data, plant functional traits* and *photosynthetic capacity* (note that we simply use the point estimates from previous models and do not consider uncertainty in these estimates). $LANDSCAPE$, FRI and $SEASON$ describe the landscape (Mopani, Satara, Skukuza, Pretoriuskop) in which the experiment was performed, the fire return interval (annual, bienniel, triennial) and the season of the experimental fire (August, October, December, February). The species name ($SPECIES$) is treated as a random effect. These model was estimated using lme4 (Bates et al. 2011). We used MCMC sampling to estimate the whether the modelled factors significantly influenced the response variates. To approximate the goodness of fit of these models we calculated the R^2 between the data and the model predictions.

Results

Tree allometry

Tree height (m) scaled on average as 0.64 of diameter (cm) (Figure 1; Supplementary Table 2 for the estimated coefficients). There were between species differences in the scaling coefficients; *Acacia nigrescens* had the highest coefficient (0.70), while *Combretum imberbe* had the lowest (0.61).

Bark thickness scaled positively with stem diameter (Figure 1, Supplementary Table 2), but as a negative allometry (the average scaling average coefficient was 0.59). This negative allometry indicates that investment in bark is high initially but decreases as trees grow larger. The scaling coefficients differed substantially between species from 0.24 for *Strychnos madagascarensis* to 0.74 for *Terminalia sericea, Dichrostachys cinerea* and *Maytenus senegalensis.* The credible intervals of the posterior estimates of the scaling coefficient for several species pairs did not overlap, suggesting that species differed significantly in how bark thickness scaled with size. The intercepts of this allometry additionally indicate that species differed significantly in mean bark thickness.

The bark moisture content scaled negatively (the average scaling coefficient was -0.35) with stem diameter (Figure 1, Supplementary Table 2). There were large and significant differences between species in the scaling coefficients and in the intercepts. Some species maintained relatively low moisture contents across all tree sizes (*Combretum apiculatum*) whereas others maintained high moisture contents in small trees, which decreased rapidly as tree size increased (*Strychnos madagascarensis*).

Wood density scaled negatively (the average scaling coefficient was -0.047) with stem diameter (Figure 1, Supplementary Table 2), but there were no significant between species differences in these scaling coefficients. The intercepts of these allometries indicated that there were differences in wood density between several pairs of species, with *Acacia nigrescens* having high wood density and *Maytenus senegalensis* having lower wood density.

Specific leaf area did not vary as a function of stem diameter (Figure 1, Supplementary Table 2) although there were significant differences between species in the mean specific leaf area.

Topkill probability

The probability of topkill was significantly influenced by tree height and the fire intensity, but not by fire season (main effects, Figure 2). Larger trees had a lower probability of topkill, while more intense fires increased the probability of topkill. The credible intervals of the effect of season of fire on topkill included zero, however individuals exposed to fires in the dry (dormant) season (August and October fires, coded as Fire-Season = 1 in the statistical model) had a lower likelihood of topkill than those exposed to fires in the wet (growing) season (December, February or April fires; coded as Fire-Season = 0 in the statistical model). The effect of tree height was greater than the effect of fire intensity and fire season (assuming typical tree heights and fire intensities for our study area). The effects of fire intensity and season were greatest for trees of intermediate (1 - 5 m) height (Figure 2). That is, irrespective of fire intensity or fire season small trees (< 0.5 m height) faced almost certain topkill, while larger trees (> 5 m height) faced negligible probability of topkill.

The data allowed us to fit topkill models to 38 common species in the data set. The fitted models revealed that species differed substantially in their topkill responses (Figure 2). The differences in topkill responses of the different species can be visualised by plotting, for each species, the predicted probability of topkill of a 2m high tree in a 2000 kW.m^{-1} August fire (a typical fire intensity in the study area; Govender et al. 2006). This plot reveals a broad range in the estimates of topkill probability, from 0.12 for *Anonna senegalensi* to 0.99 for *Euclea natalensis* (Figure 3).

Fire induced mortality rates were generally low. For the 38 species for which we fitted topkill models, only 13 species suffered any mortality (the highest rate was 0.046 for *Acacia gerradii*). Only 8 of these had mortality rates > 0.01. The mortality rates are depicted in Figure 3.

The probability of topkill of a 2m tall tree in a standard fire was negatively related to its diameter (Figure 4, $F_{1,12}$=7.59, p=0.017, adjusted R-squared = 0.34). This effect was not significantly influenced by the scaling coefficient ($F_{1,12}$=0.267, p=0.62, adjusted R-squared = 0.02) or by the intercept ($F_{1,12}$=0.04, p=0.83, adjusted R-squared = 0.004) of the height-diameter allometry, implying that the influence of stem diameter on topkill probability was caused by the combination of scaling coefficient and intercept.

The strength of the effect of tree height on the probability of topkill was greater for species that had drier bark (Figure 5, $F_{1,12}$=32.0, $p<0.001$, adjusted R-squared = 0.70), that is species with moister bark were less susceptible to topkill. The bark thickness of a 2 m tall tree had no effect on the probability of topkill of a 2 m tree ($F_{1,12}$=1.71, p=0.22, adjusted R-squared = 0.05), nor on the sensitivity of topkill to changes in height ($F_{1,12}$=1.23, p=0.29, adjusted R-squared = 0.02). The sensitivity of the height effect on topkill was influenced by the volume of water stored in the bark (indexed as the product of bark volume and bark moisture content) but not by the bark volume ($F_{1,12}$=0.04, p=0.74, adjusted R-squared = 0.009) implying that the moisture content alone is, in our data, an adequate predictor.

Leaf level physiology

Although there was substantial variation between species in the parameter estimates for Γ^*, R, and V_{cmax} there was overlap in the credible intervals of the posterior estimates (Figure S1). J_{max} and g_m did differ significantly between species. The instantaneous water use efficiency (calculated as the ratio of photosynthesis to stomatal conductance at ambient CO_2 concentrations) was positively correlated with foliar δ^{13}C (Figure S2, $F_{1,11}$=12.45, p=0.0047, adjusted R-squared = 0.49) and the ratio of J_{max} to V_{cmax} was negatively correlated with foliar δ^{15}N (Figure S2, $F_{1,11}$=13.11, p=0.0040, adjusted R-squared = 0.50). The specific leaf area was not related to any of these ecophysiological parameters or to foliar δ^{13}C, leaf nitrogen content, or to the leaf C:N ratio (analyses not shown); it was, however, significantly positively related to foliar δ^{15}N (Figure S2, $F_{1,11}$=15.07, p=0.0022, adjusted R-squared = 0.52).

Changes in tree density

We examined the extent to which changes in tree density, the change in density of large trees and the change in the proportion of large trees changed over time. In these analyses we analyse the changes for each of 176 plots in the experiment (all plots bar the fire exclusion plots), including only cases where there were at least 25 individuals present in the first survey. We treat species identity as random effects. Since we only have density and topkill data for 25 species, leaf-trait / allometric data for 13 species and gas exchange data for 14 species, we run 3 separate analyses for each of these subsets of the data.

The results of these analyses (Table 1) show that the landscape in which the experiment was replicated was a significant factor in almost all models. The fire treatments (fire return interval and fire season) did not significantly influence the response variates. Species that increased in tree density had lower bark thickness, moister bark and lower Γ^* (the CO_2 compensation point of photosynthesis). Species that showed increases in the density of large (>2m) trees had lower Γ^* and higher water use efficiency. Species where the population shifted to being more dominated by large (>2m tall) individuals had lower sensitivity of topkill to fire intensity, thicker bark, higher bark moisture and higher water use efficiencies.

Discussion

Allometries have been successfully used to interpret allocation patterns and the selective pressures encountered in forest environments (O'Brien et al. 1995; Alves & Santos 2002; Poorter et al. 2006). However, despite empirical evidence suggesting that different fire regimes select for different allometric relationships (Archibald & Bond 2003), few authors have attempted to relate plant responses to savanna fires with allometries constructed from traits hypothesised to determine vulnerability to fire injury. Here we have shown that the allometries of height, diameter and bark properties can determine the vulnerability of woody plants to fire.

All species in our study had negative bark-thickness - diameter allometries, which suggests that there is a higher initial investment in bark in small trees, but that this investment decreases with size. A negative bark allometry is theoretically expected in environments prone to surface fires (Jackson et al. 1999) and has been reported in savannas by Hoffmann et al. (2003). In environments where fire is rare or not severe the allometries are often positive (Jackson et al. 1999, Hoffmann et al. 2003).

Our data show that fire intensity and tree size influence the probability of topkill. However, our results indicate that the effects of tree size overwhelm the effects of fire intensity in our study system. Fire intensity is only of importance for small individuals and between species differences are not apparent for very small (<0.5 m tall) and for very large (>5 m tall) individuals. We found, as did Schwilk et al. (2006) in a conifer forest in the Sierra Nevada, that fire season had little effect on the topkill responses of the different species. Overall we found a weak but insignificant effect of fire season. This result contrasts with Williams et al. (2009) who detected substantial fire season effects and with the expectation that fires during the metabolically active period should be more damaging

(Midgley et al. 2010).

Our study showed that species differed quite considerably in their likelihood of topkill for 2 m tall tree in a typical (dry season, 2000 kW/m) fire. The likelihood of topkill of a 2 m tall tree in one of these typical fires was clearly related to its diameter, that is to the allometry between height and diameter. Specifically, species with larger diameters for a given height were less likely to be topkilled. One might anticipate that this might simply be because larger diameter trees have thicker bark. Surprisingly and in contradiction to previous studies (e.g. Hoffmann et al. 2003, Hoffmann et al. 2009, Lawes et al. 2011) we however found that between species variation in bark thickness of 2 m tall tree explained no variance in their probability of topkill, or in the sensitivity of topkill to changes in tree size. This may be because species in our study had such similar bark allometries, that other factors are more important. This view is partly supported by the observation that the allometries presented in Hoffmann et al. (2003) were more variable than those reported here. Alternatively, it may simply be that it is not possible or economic to protect epicormic buds with thick bark in this environment. Hence, species may instead rely on basal resprouting and abstain from investing in epicormic buds and thick bark. What we did find was that the probability of topkill for species with higher bark moisture contents was less sensitive to plant height. Hence, the data from this study support the view that bark moisture content and how stem diameter scales with height influence topkill. This contrasts with studies that assume that bark thickness is of over-riding importance (Harmon 1984, Uhl and Kaufmann 1990, Pinard and Huffman 1997, Lawes et al. 2011). Notable here is Hoffmann and Solbrig (2003), who found that a bark thickness of 6·5 mm ensured 50% stem survival of trees in low-intensity savanna fires. Our findings also contrast with Midgley et al. (2010) who argued that stem thickness has little influence on fire tolerance because of the low thermal conductivity of wood (Midgley et al. 2010).

Models of the heat transfer process have been used to argue that bark moisture content is unimportant (Michaletz and Johnson 1997, Midgley et al. 2010). However Jones et al. (2004, 2006) illustrate that bark moisture can have a dominant effect on stem temperatures. Their model considers not only the conductivity of water but also the heat absorption associated with phase change and illustrates that the evaporation of water within the bark forms a protective barrier against critical temperature increases. We are aware of no empirical studies that suggest that bark moisture content has a more important effect than bark thickness on stem damage. Pinard and Huffman (1997) show that moisture content had a significant effect on peak cambial temperature, even though the effect of bark thickness explained a greater proportion of the variance. Similarly, Vines (1968) showed that bark moisture explained only residual variance, not explained by bark thickness.

The consequences of fire tolerance for changes in species abundance are seldom investigated in savannas (see Keith et al. 2007 for an example from Australian heathlands). Nefabas and Gambiza (2007) found that species with thinner bark had lower resprouting rates after fire and decreased in abundance on burnt plots in a long term burning experiment in a miombo savanna. We found that species where the probability of topkill was more strongly influenced by tree height decreased more in density. Additionally thick bark and moister bark was associated with increases in tree density. Species less sensitive to fire intensity were associated with greater increases in the proportion of large trees, whereas species with thick and moist bark were characterised by shifts towards more large individuals.

Fire intensity and response to fire are not the only factors of importance in savanna tree dynamics. In fact, Gignoux et al. (1997) suggest that a capacity for rapid growth may be a recipe for success in fire prone environments. We found that species with lower CO_2 compensation points for photosynthesis (the compensation point is indicative of the level of photo-respiration; von Caemmerer 2000) tended to increase in density and that species with higher water use efficiencies were characterised by shifts towards more large individuals. That is, aspects of the leaf level carbon economy are related to the ecological success of tree species in our study system.

In conclusion we found that savanna species differ considerably in their fire tolerance. We show that tree species that have high bark moisture contents and species that had thicker stems when shorter were more fire tolerant. Bark thickness, was surprisingly unimportant. We were further able to show that changes in species abundance were related to fire tolerance. However, the influence of parameters describing fire tolerance on the abundance and structure of the surveyed populations was complex. This may be because there is only a small window of tree sizes (circa 1 - 4 m) for which differences in topkill are apparent. This implies that the rate at which individuals move through this critical size window is important. This is a restatement of Gignoux et al.'s (1997) theory that rapid growth may be a successful strategy in fire prone savannas. Direct measurements of growth rates of savanna trees are needed to explore this theory.

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Table 1. Significant effects (estimated using MCMC methods) for three linear mixed effects models that examine associations between change in tree density, the density of large (>2 m tall) trees and the dominance index (the relative proportion of large trees of the study species) and plant functional traits on experimental plots exposed to fire. The data originate from a long term burning experiment (experimental factors in this experiment were landscape, fire return interval and fire season).

	change in density	change in large trees	change in dominance index
		Topkill parameters	
R^2	0.64	0.49	0.56
	p-value	p-value	p-value
(Intercept)	0.695	0.000	0.904
height[1]	0.295	0.101	0.643
fire intensity[1]	0.795	0.282	**0.041**
fire season[1]	0.637	0.404	0.794
Landscape[3]	**0.000**	**0.000**	**0.013**
FRI[4]	0.330	0.994	0.710
Fire Season[5]	0.825	0.467	0.108
		Leaf and stem parameters	
R^2	0.66	0.57	0.59
	p-value	p-value	p-value
(Intercept)	0.270	0.211	0.308
height[2]	0.070	0.080	0.387
bark thickness[2]	**0.004**	0.853	**0.010**
SLA[2]	0.228	0.533	0.136
wood density[2]	0.730	0.524	0.128
bark moisture[2]	**0.011**	0.996	**0.050**
Foliar N	0.416	0.116	0.057
Foliar δ^{15}N	0.733	0.961	0.313
Foliar δ^{13}C	0.841	0.530	0.093
Landscape[3]	**0.000**	**0.000**	0.300
FRI[4]	0.362	0.878	0.585
Fire Season[5]	0.989	0.467	0.300
		Gas exchange parameters	
R^2	0.64	0.66	0.60
	p-value	p-value	p-value
(Intercept)	0.027	0.000	0.434
R	0.778	0.051	0.977
$\Gamma*$	**0.027**	**0.000**	0.405
g_m	0.092	0.076	0.432
J_{max}/V_{cmax}	0.304	0.805	0.832
WUE	0.177	**0.035**	**0.000**
Landscape[3]	**0.000**	**0.000**	0.054
FRI[4]	0.164	0.242	0.779
Fire Season[5]	0.370	0.261	0.276

1. height, fire intensity and fire season indicate the effects of these factors on the probability of topkill
2. height, bark thickness, SLA, wood density, bark moisture refer to the intercepts of the allometric equations illustrated in Figure 1 and Supplementary Table 2
3. landscape indicates one of 4 landscapes (regions) in which the experiment was replicated
4. FRI indicates the experimental fire return interval (annual, biennial, triennial)
5. Fire Season indicates the month of experimental fires (August, October, December, February, April)

Table S1. Names of species used in this study and abbreviations used in the tables and figures. Names follow Palgrave (1983).

Name	Abbreviation	Alt. abbreviation
Acacia exuvialis	ACAEXU	Aexu
Acacia gerrardii	ACAGER	Ager
Acacia nigrescens	ACANIG	Anig
Acacia tortilis	ACATOR	Ator
Annona senegalensis	ANNSEN	Asen
Cassia petersiana	CASPET	Cpet
Cissus cornifolia	CISCOR	Ccor
Colophospermum mopane	COLMOP	Cmop
Combretum apiculatum	COMAPI	Capi
Combretum collinum	COMCOL	Ccol
Combretum hereroense	COMHER	Cher
Combretum imberbe	COMIMB	Cimb
Combretum molle	COMMOL	Cmol
Combretum zeyheri	COMZEY	Czey
Dalbergia melanoxylon	DALMEL	Dmel
Dichrostachys cinerea	DICCIN	Dcin
Dombeya rotundifolia	DOMROT	Drot
Ehretia amoena	EHRAMO	Eamo
Euclea natalensis	EUCNAT	Enat
Grewia bicolor	GREBIC	Gbic
Grewia monticola	GREMON	Gmon
Lonchocarpus capassa	LONCAP	Lcap
Maytenus heterophylla	MAYHET	Mhet
Maytenus senegalensis	MAYSEN	Msen
Mundulea sericea	MUNSER	Mser
Ochna natalitia	OCHNAT	Onat
Ormocarpum trichocarpum	ORMTRI	Otri
Ozoroa reticulata	OZORET	Oret
Parinari curatellifolia	PARCUR	Pcur
Pavetta schumanniana	PAVSCH	Psch
Peltophorum africanum	PELAFR	Pafr
Pterocarpus rotundifolius	PTEROT	Prot
Sclerocarya birrea	SCLBIR	Sbir
Securinega virosa	SECVIR	Svir
Senna petersiana	SENPET	Spet
Strychnos madagascariensis	STRMAD	Smad
Terminalia sericea	TERSER	Tser
Xerophyta obovata	XEROBO	Xobo
Ximenia caffra	XIMCAF	Xcaf
Ziziphus mucronata	ZIZMUC	Zmuc

Table S2. Regression coefficients for the allometric models depicted in Figure 1. Units are as defined in the Figure 1. $\bar{x}$ indicates the the mean of the posterior distribution of the estimate estimate, LCI the lower credible interval (0.025) and UCI the upper (0.975) credible interval. Abbreviations of the species names are defined in supplementary Table 1. For the specific leaf area (SLA) model the slope was not different from zero, we therefore only list the estimates for the intercept.

	Height (m) ˜ Diameter (cm)						Bark thickness (mm) ˜ Diameter (cm)					
	slope			intercept			slope			intercept		
Species	$\bar{x}$	LCI	UCI	$\bar{x}$	LCI	UCI	$\bar{x}$	LCI	UCI	$\bar{x}$	LCI	UCI
ACANIG	**0.70**	0.63	0.78	**-0.01**	-0.11	0.07	**0.69**	0.61	0.76	**0.26**	0.17	0.36
COMAPI	**0.64**	0.55	0.72	**0.05**	-0.02	0.13	**0.54**	0.40	0.68	**-0.06**	-0.17	0.05
COMCOL	**0.63**	0.54	0.70	**0.03**	-0.04	0.12	**0.49**	0.37	0.60	**0.34**	0.25	0.44
COMHER	**0.63**	0.56	0.70	**0.00**	-0.07	0.07	**0.62**	0.52	0.71	**0.29**	0.20	0.37
COMIMB	**0.61**	0.52	0.68	**-0.04**	-0.12	0.07	**0.48**	0.35	0.60	**0.32**	0.18	0.47
COMZEY	**0.62**	0.53	0.69	**-0.01**	-0.08	0.07	**0.61**	0.49	0.73	**0.19**	0.09	0.29
DICCIN	**0.65**	0.57	0.75	**-0.06**	-0.12	0.00	**0.74**	0.59	0.89	**0.29**	0.20	0.37
GREBIC	**0.61**	0.49	0.70	**-0.04**	-0.10	0.02	**0.71**	0.52	0.92	**0.14**	0.02	0.24
LONCAP	**0.64**	0.56	0.73	**-0.12**	-0.21	-0.03	**0.44**	0.33	0.55	**0.34**	0.23	0.45
MAYSEN	**0.64**	0.56	0.73	**-0.04**	-0.09	0.02	**0.74**	0.61	0.87	**0.12**	0.05	0.18
PELAFR	**0.65**	0.58	0.73	**-0.03**	-0.10	0.03	**0.61**	0.49	0.73	**0.34**	0.24	0.44
SCLBIR	**0.65**	0.59	0.74	**-0.08**	-0.20	0.00	**0.56**	0.45	0.67	**0.48**	0.32	0.64
STRMAD	**0.64**	0.57	0.71	**-0.04**	-0.11	0.03	**0.24**	0.13	0.36	**0.27**	0.18	0.37
TERSER	**0.63**	0.56	0.69	**-0.02**	-0.08	0.04	**0.74**	0.66	0.82	**0.22**	0.14	0.30

	Wood density (kg.m^{-3})˜ Diameter						Bark moisture (%) ˜ Diameter (cm)						SLA (cm^{-2}mg^{-1})		
	slope			intercept			slope			intercept			intercept		
Species	$\bar{x}$	LCI	UCI	$\bar{x}$	LCI	UCI	$\bar{x}$	LCI	UCI	$\bar{x}$	LCI	UCI	$\bar{x}$	LCI	UCI
ACANIG	**-0.02**	-0.07	0.04	**1.07**	1.00	1.14	**-0.22**	-0.37	-0.07	**0.83**	0.63	1.02	**1.88**	1.84	1.91
COMAPI	**-0.04**	-0.13	0.04	**1.00**	0.94	1.07	**-0.06**	-0.33	0.21	**0.36**	0.15	0.58	**1.95**	1.91	1.99
COMCOL	**-0.02**	-0.09	0.06	**0.87**	0.80	0.93	**-0.49**	-0.73	-0.27	**1.31**	1.12	1.51	**1.90**	1.87	1.94
COMHER	**-0.03**	-0.09	0.04	**0.98**	0.92	1.04	**-0.27**	-0.45	-0.09	**0.77**	0.61	0.93	**1.84**	1.81	1.88
COMIMB	**-0.04**	-0.12	0.04	**1.01**	0.92	1.11	**-0.17**	-0.43	0.09	**0.53**	0.22	0.84	**1.89**	1.85	1.92
COMZEY	**-0.14**	-0.24	-0.05	**0.96**	0.89	1.04	**0.04**	-0.21	0.30	**0.64**	0.42	0.86	**1.91**	1.87	1.94
DICCIN	**0.01**	-0.08	0.11	**0.94**	0.88	0.99	**-0.48**	-0.77	-0.18	**1.07**	0.90	1.25	**1.78**	1.75	1.81
GREBIC	**-0.02**	-0.12	0.10	**1.01**	0.94	1.07	**-0.34**	-0.73	0.06	**0.62**	0.40	0.84	**1.86**	1.83	1.90
LONCAP	**0.00**	-0.08	0.07	**0.91**	0.83	0.98	**-0.42**	-0.65	-0.21	**1.32**	1.09	1.54	**1.79**	1.75	1.83
MAYSEN	**-0.10**	-0.19	-0.02	**0.83**	0.78	0.88	**-0.18**	-0.43	0.07	**1.10**	0.97	1.24	**1.81**	1.78	1.85
PELAFR	**-0.10**	-0.18	-0.02	**1.03**	0.96	1.10	**-0.29**	-0.52	-0.06	**0.79**	0.59	0.98	**1.82**	1.79	1.86
SCLBIR	**-0.09**	-0.17	-0.02	**0.89**	0.79	0.99	**-0.33**	-0.55	-0.10	**1.40**	1.08	1.71	**1.79**	1.76	1.83
STRMAD	**-0.09**	-0.16	-0.02	**0.97**	0.91	1.04	**-1.05**	-1.29	-0.81	**2.18**	1.97	2.39	**1.86**	1.83	1.90
TERSER	**0.00**	-0.06	0.06	**0.85**	0.79	0.91	**-0.70**	-0.86	-0.54	**1.21**	1.07	1.37	**1.85**	1.82	1.88

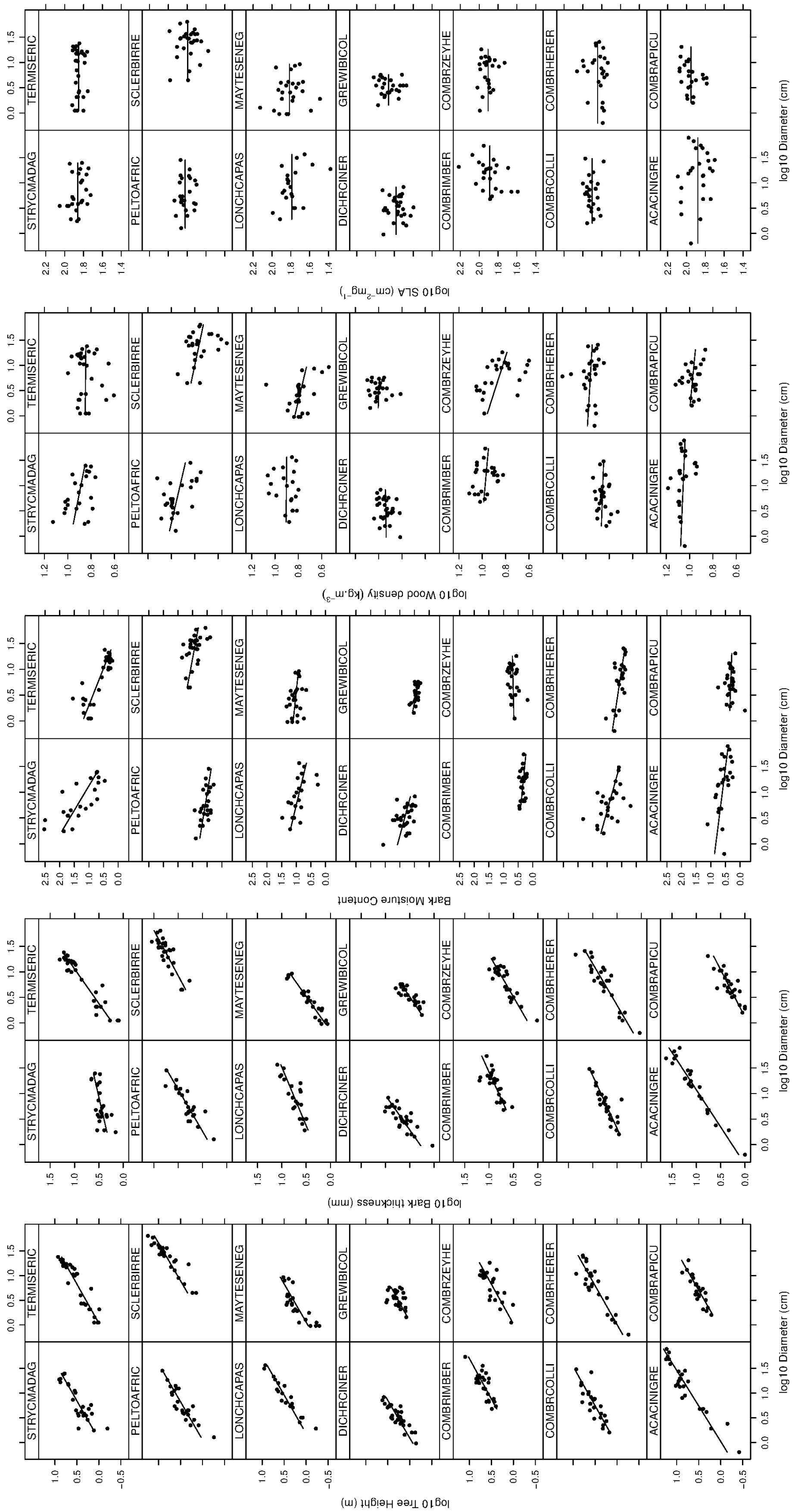

Figure 1: Allometric relationships between stem diameter, tree height, bark thickness, bark moisture content, wood density and specific leaf area for common savanna trees. The estimated regression coefficients and their coefficients are indicated in supplementary Table 2. Abbreviations of the species names are defined in supplementary Table 1.

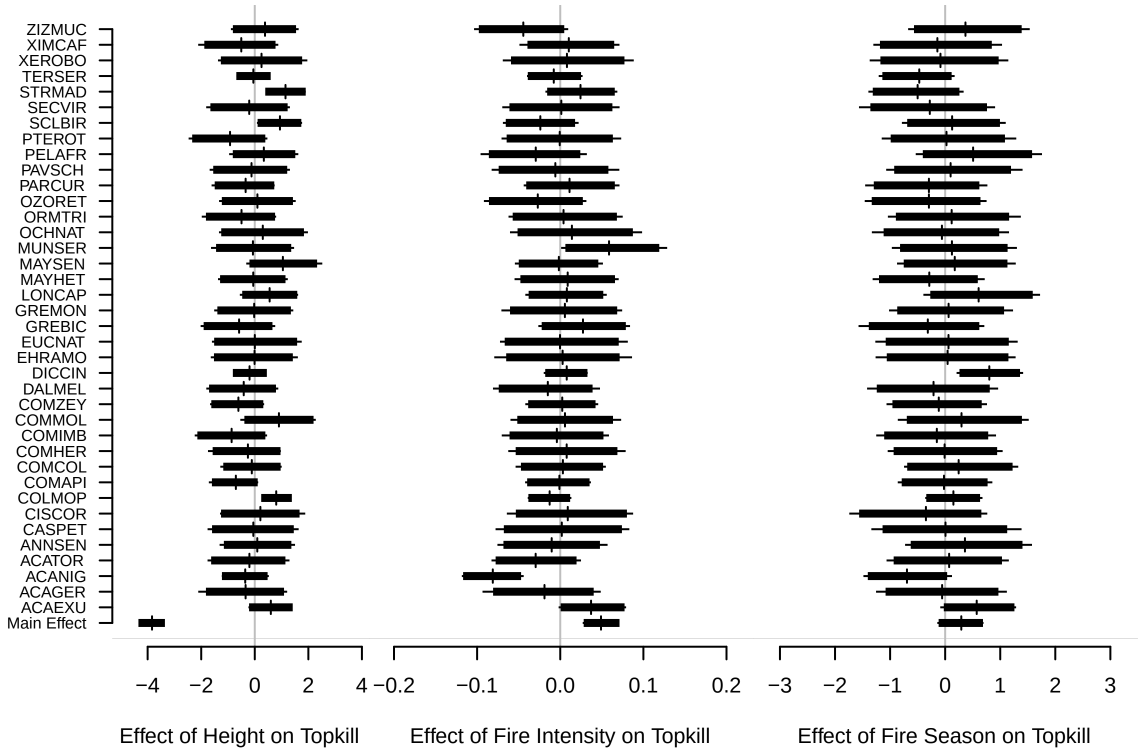

Figure 2: Posterior mean (vertical ticks), 90% (thick bars) and 95% (thin bars) estimates of the effect of tree height (log tree height in m), fire intensity (square root intensity in kW.m^{-1}) and the effect of burning in the wet season (coded as 1) as apposed to the dry season (coded as 0) on the logit of the probability of topkill for common savanna tree species. The main effects are the species independent effects, the species effects display the extent to which the species deviate from the mean effect observed over all species. The abbreviations for the species names are explained in supplementary Table 1.

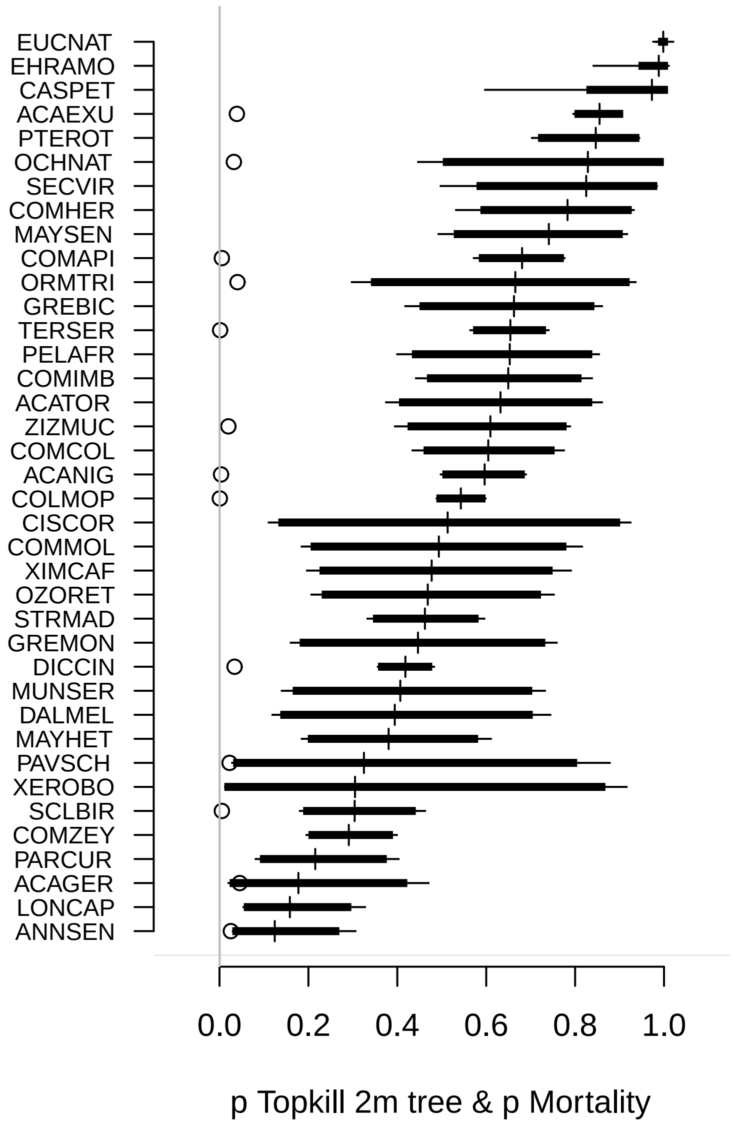

Figure 3: Ranked distribution of the probability of a 2 m tall tree being killed in a dry season fire with an intensity of 2000 kW.m^{-1} for common savanna tree species. The 90 % (thick bars) and 95% (thin bars) credible intervals are propagated from the models illustrated in Figure 2. The circles indicate the mortality probabilities, for species for which no mortality was observed no circle is plotted. The abbreviations for the species names are explained in supplementary Table 1.

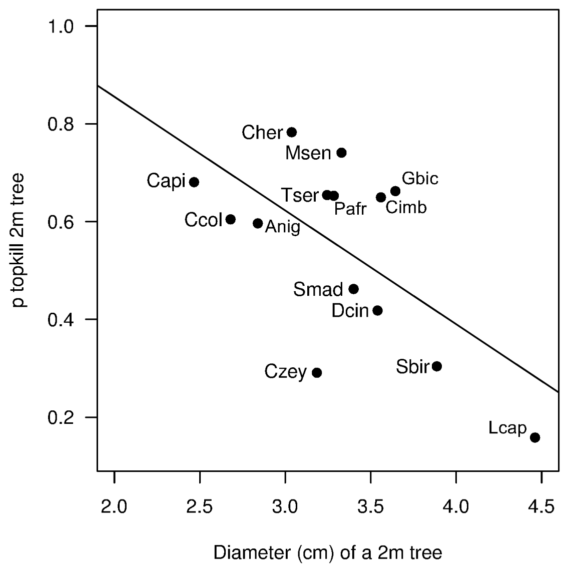

Figure 4: The relationship (solid line) between the stem diameter of a 2m tall tree (estimated from the allometric models in Figure 1) and the probability of topkill of a 2m tall tree in a dry season fire of 2000 kW.m^{-1} fire for common savanna tree species. The labels indicate the species names (see supplementary Table 1).

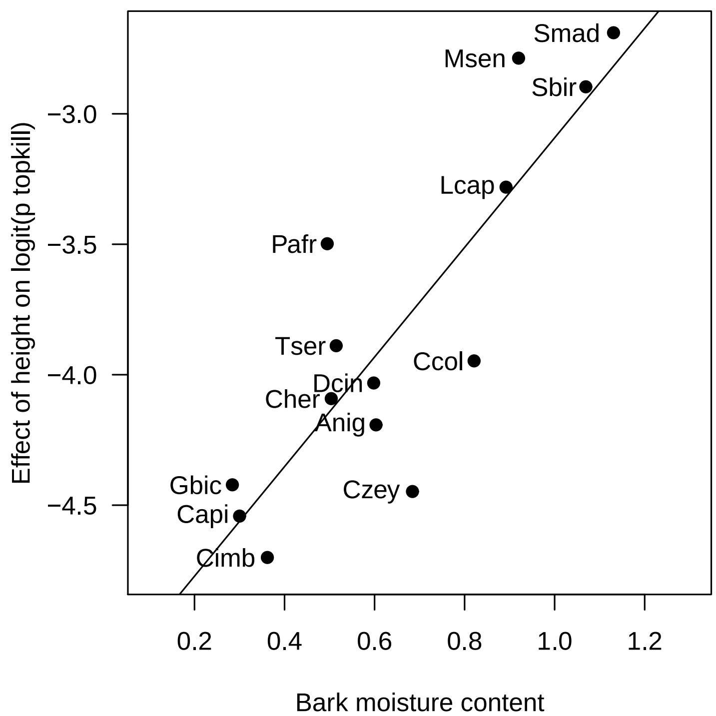

Figure 5: The relationship (solid line) between the bark moisture content and sensitivity of the logit of probability of topkill to tree height for common savanna tree species. The labels indicate the species names (see supplementary Table 1)

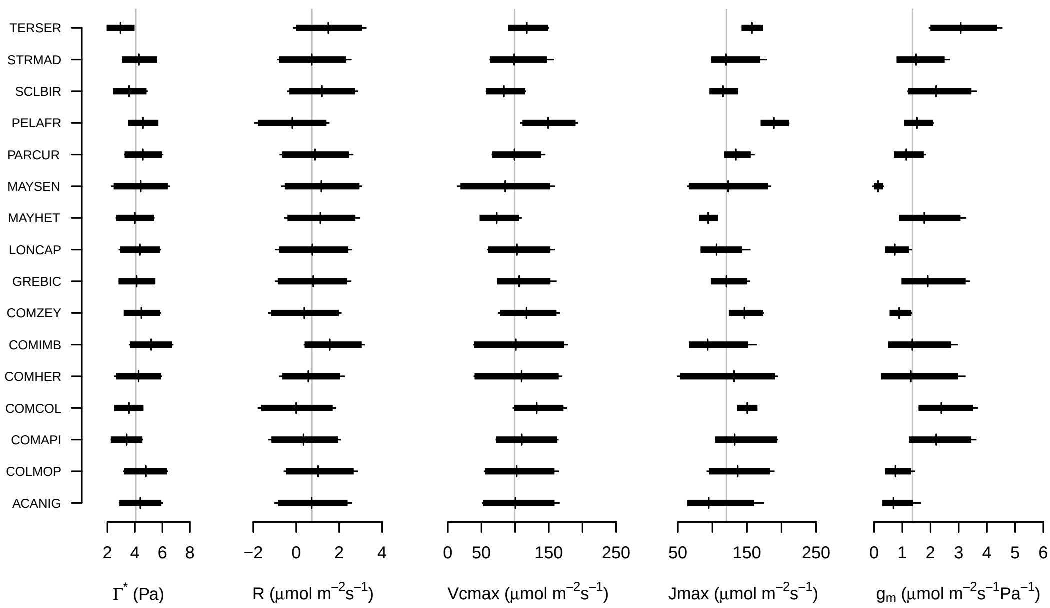

Figure: S1: Posterior mean (vertical ticks), 90% (thick bars) and 95% (thin bars) estimates of the CO_2 photo-compensation point Γ^*, the mitochondrial respiration in light R, maximum rate of Rubisco carboxylation V_{cmax}, maximal electron transport rate J_{max} and the conductance for CO_2 diffusion from inter-cellular airspace to site of carboxylation g_m for common savanna tree species. The abbreviations for the species names are explained in supplementary Table 1.

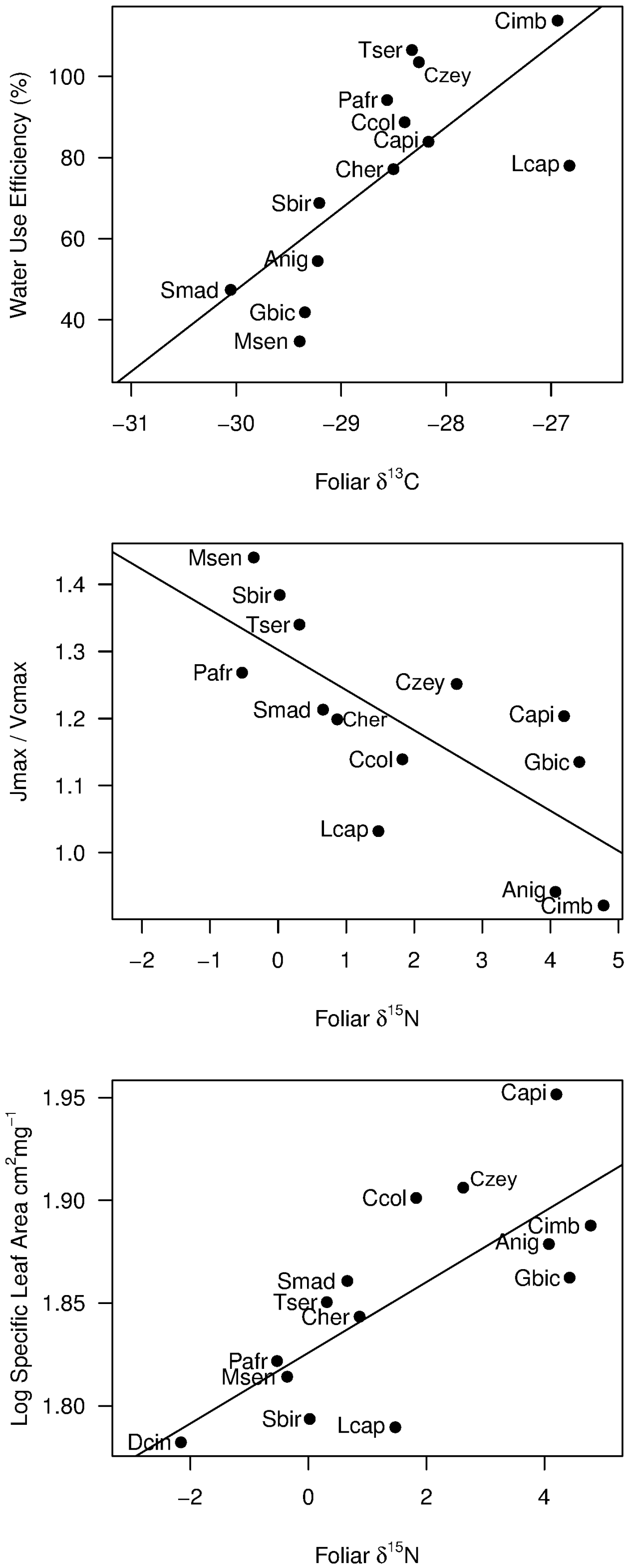

Figure: S2: The relationship between water use efficiency, estimate from gas exchange measurements and foliar δ^{13}C; the ratio of $Jmax$ to $Vcmax$ and foliar δ^{15}N; and the relationship between specific leaf area and foliar δ^{15}N for common savanna tree species. The vertical grey lines are the mean parameter estimate across all species. The labels indicate the species names (see supplementary Table 1)