THE EFFECT OF DIFFERENT FIRE TREATMENTS ON THE POPULATION STRUCTURE AND DENSITY OF THE MARULA (*SCLEROCARYA BIRREA* SUBSP. *CAFFRA*) IN THE KRUGER NATIONAL PARK.

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Abstract

To determine the influence of frequency and season of burn on the growth structure and density of *Sclerocarya birrea* (A. Rich) Hochst. subsp. *caffra* (Sond. Kokwaro), six replicated fire treatments of the experimental burning plot trial were surveyed in the *Sclerocarya birrea/Acacia nigrescens* savanna of the central Kruger National Park. Studies were also conducted in an exclosure to determine the success of recruitment of *Sclerocarya birrea* (marula) individuals across a range of fire intensities in the absence of herbivory. The results indicated that the lower canopy structure (individuals <2 m) was greatly affected by fire, whereas density was unaffected. The lower canopy generally responded to the interaction between frequency and season, and not to the main effects of season or frequency. August triennial burns had the greatest impact on the total seedling structure, with higher fire intensities resulting in the development of a multi-stemmed morphology.

Keywords: fire frequency, fire intensity, fire season, management fire, prescribed fire, savanna.

Introduction

The visual appearance of the woody vegetation over much of the Kruger National Park confirms that there has been a significant decline in the density of large trees in the Kruger National Park (Viljoen 1988). Preliminary examination of certain scenes from the fixed- point- photo series suggests that, particularly on basaltic soils, a marked decline of mature marula tree numbers has occurred over the past eighteen years and that recruitment is not taking place. This is possibly due to an interaction between fire and elephants. It is hypothesised that elephants are killing the mature marula trees by debarking or pushing them over, while fire is preventing young trees from establishing. Norton-Griffiths (1979) found that fire could hold woody plant recruitment rates well below mortality rates even at burning rates that were considered conservative. As part of an investigation into the population structure of the marula trees in the Kruger National Park, the effect of season and frequency of burning, as well as fire intensity, on this tree species was studied. The main objective of this study was to determine the effect of fire management on the structure and density of the marula population of the Kruger National Park, and to determine the success of recruitment of marula individuals in the absence of herbivory. Studies on marula populations were conducted on the experimental burn plot trial in the *Acacia nigrescens/Sclerocarya birrea* savanna and in the Hlangwine exclosure at Pretoriuskop in the Kruger National Park.

Trollope (1980) concluded that fire favours the development and maintenance of a predominantly grassland vegetation by suppressing the development of juvenile trees and shrubs, and preventing the development of more mature plants to a taller fire-resistant stage. The response of vegetation to fire, heavily depends upon fire frequency, seasonality and intensity (Bailey 1988). During a trial to study the effects of different burning frequencies on the density and composition of the woody vegetation in semi-arid savanna in eastern Botswana, Sweet (1982) found that growth of woody plant species and coppice was suppressed by frequent burning.

Fire intensity is a measure of energy released in fires, which varies with fuel moisture content, wind and slope conditions under which the fires burn. The different fire types (headfires, backfires and ground fires) will also affect fire intensity (Trollope 1983). There is a highly significant correlation between fire intensity and topkill (Trollope 1983; Trollope, Trollope, Biggs, Pienaar &

Potgieter 1998b). The main effect of fire on the woody component is to cause topkill of stems and branches, forcing the plants to coppice from the collar region of the stem (Trollope, Potgieter & Zimbatis 1995b). Trollope (1983) found that a hot fire of approximately 2500 kJ. $s^{-1}.m^{-1}$ was necessary to cause a significant topkill of bush to a height of 2 m, and that the topkill of bush does not increase appreciably when fire intensities are greater than 2500 $kJ.s^{-1}.m^{-1}$. Shrubs and seedlings in the <0.5 m height class, however, suffered a significant topkill of stems and branches, irrespective of the fire intensity (Trollope 1983). Trollope *et al.* (1995b) found the threshold height for woody vegetation within the Kruger National Park to be 3 m.

Trollope *et al.* (1995b) further showed that the woody vegetation of the Kruger National Park was not sensitive to season of burning, but that burning frequency seems to have dramatic effects on woody plant phytomass (Trollope *et al.* 1998b). Trollope *et al.* (1998b) stated that the physiological state of the plants rather than the time of year determines the reaction of plants to fire. The average mortality of 14 of the most common bush species in the Kruger National Park that were subjected to fire intensities ranging from 110 to 6704 $kJ.s^{-1}.m^{-1}$ was only 1.3 % (Trollope *et al.* 1995b). The mortality rate of the marula was 0.53% after being subjected to fire intensities >2000 $kJ.s^{-1}.m^{-1}$. Fire therefore, might not necessarily have an impact on the species diversity, but could alter the structure of the woody component (Trollope, Biggs, Potgieter & Zimbatis 1995a).

Van der Schijff (1957) initiated an experimental program of fire research in the Kruger National Park in 1954, where the objectives of this program were to determine the effects of season and frequency of burning on the four major landscapes of the Kruger National Park (Brynard 1972; Van Wyk 1972). The cumulative effect of up to 46 years of different combinations of seasons and frequencies of burning provides a unique opportunity to determine the long-term effects of these treatments on the vegetation of the Kruger National Park, and on the reaction of specific species to different fire treatments (Trollope, Potgieter & Trollope 1998a). Van Wilgen (1987) expressed the need for autecological studies on key plant species on these experimental plots in order to interpret the results of the various treatments.

Study area and experimental design

The Kruger National Park is situated in the Lowveld regions of Mpumalanga and the Northern Province of South Africa bordering on Mozambique. It covers an area of 18 998 km^2. The climate is subtropical with warm wet summers and mild winters, seldom experiencing frost. Annual rainfall varies from 750 mm in the south to 350 mm in the north. The pattern of rainfall over the past century has been characterised by extended wet and dry periods with cycles of about 10 years. A variety of formations, soil types and climatic conditions support a diversity of vegetation types, varying from open savanna to dense woodland. These climatic factors have marked effects on the dynamics of the ecosystem, and on the occurrence of fires (Van Wilgen, Biggs & Potgieter 1998).

Data were collected on certain treatments of the experimental burn plots (Satara, Nwanetsi, Marheya and Lindanda replications) located in the *Sclerocarya birrea/Acacia nigrescens* savanna landscape (Figure 15), which is one of the largest landscapes of the Kruger National Park, covering approximately 7.2 % of the total area. This landscape is described as a semi-arid, basaltic lowveld (Coetzee 1983) with deep, red vertic clay soils (Arcadia form) on the footslopes and in the valley bottom (Venter 1990). The long-term (n = 35 years) average rainfall at Satara is 548 mm (Gertenbach 1983). See Appendix I for a list of the dominant woody species on each of the treatments of these replicates used in this study.

Experimental Burn Plots

The experimental burn plot trial was initiated in 1954 in four of the major landscapes of the Kruger National Park. Four replicates of this experiment were laid out in each of the following landscapes of Gertenbach (1983): the Lowveld Sour Bushveld of Pretoriuskop; the *Combretum spp/Terminalia sericea* woodland; the *Sclerocarya birrea/Acacia nigrescens* savanna; and the *Colophospermum mopane* shrub. Each replicate consists of 14 contiguous experimental plots, with each plot being approximately seven ha in size and subjected to different burning treatments. Treatments were randomly assigned within the replicate, such that the spatial layout of treatments within each replicate was different (Trollope *et al.* 1998a). The plots are protected from fire by a double width firebreak. Treatments comprise resting the veld (fire exclosure), and burning in autumn, winter, spring and summer on an annual, biennial, triennial, quadrennial and sexennial basis (Trollope & Potgieter 1985). The quadrennial and sexennial October treatments were initiated in 1979 by dividing the biennial and triennial February plots respectively in half. The plots of these four treatments are therefore half the size (3.5 ha) of the others.

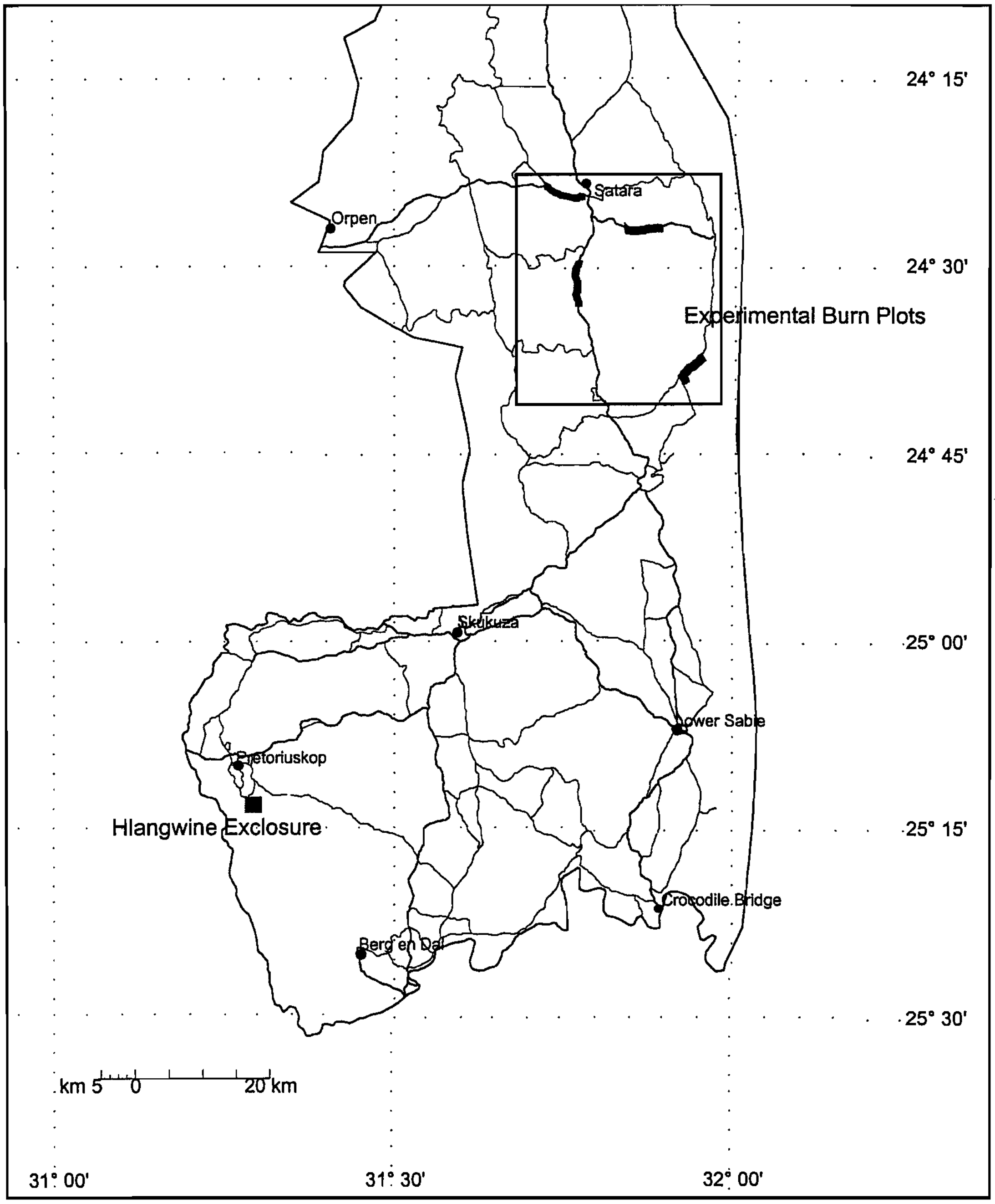
Unpublished data (Trollope 1998)[1], also analysed in this study, were collected from 43 plots that were chosen from the replicates of the experimental burn plot trial located in three of the major vegetation types in the Kruger National Park, namely the Lowveld Sour Bushveld of Pretoriuskop, the *Combretum collinum/Combretum zeyheri* woodland near Skukuza and the *Sclerocarya birrea/Acacia nigrescens* savanna.

Hlangwine Exclosure

A separate study was conducted in the Hlangwine exclosure located in Landscape 1, the Lowveld Sour Bushveld in the southern moist savanna near Pretoriuskop. This landscape, as described by Gertenbach (1983), covers approximately 2.8 % of the Kruger National Park and has an annual rainfall that varies between 600 and 1000 mm. The high soil moisture causes the grass to sprout even during winter. Soils of this landscape are sandy, mainly of the Hutton and Clovelly forms. The vegetation structure of the uplands is an open tree savanna with relatively low shrubs. *Terminalia sericea* and *Dichrostachys cinerea* subsp. *africana* dominate the woody component (Gertenbach 1983). The field layer is tall (1-2 m) and is dominated by sour grass species such as *Hyperthelia dissoluta, Elionurus muticus* and *Hyparrhenia hirta*. The bottomlands in the landscape are narrow and consist of an open savanna with single trees and sparse shrubs with a denser grass cover (Gertenbach 1983). The marula is noted as an important tree species associated with this landscape.

The Hlangwine exclosure (Figure 15), which is divided into six blocks, was established in 1973 and comprises 269 ha. Each block is approximately 700 m x 500 m. The dominant woody species in the Hlangwine exclosure are *Terminalia sericea* and *Dichrostachys cinerea* subsp. *africana*.

[1] TROLLOPE, W.S.W. 1998. Unpublished data from post-burn surveys conducted in the Kruger National Park during 1987. Dept. Livestock and Pasture Science, University of Fort Hare, Alice.



Landscape 5=Mixed *Combretum/Terminalia sericea* woodland, 12= *Colophospermum mopane/Acacia nigrescens* savanna, 17= *Sclerocarya birrea/Acacia nigrescens* savanna, 23= *Colophospermum mopane* shrubveld

Figure 15. Location of the experimental burn plots (Satara, Nwanetsi, Marheya and Lindanda replications) and the Hlangwine exclosure in the Kruger National Park.

Methods

Data collection

Experimental Burn Plot trial

To study the effect of the different components of the fire regime on the structure and density of marula individuals, data were collected from the following replicated treatments of the experimental burning plot trial:

- August (A1) - annual burn
- August (A2) - biennial burn
- August (A3) - triennial burn
- February (F2) - biennial burn
- February (F3) - triennial burn
- October (O6) - sexennial burn
- Fire exclosure (XC) - no burn

The treatments used were chosen mainly to include those that are applied when the vegetation is usually physiologically dormant and physiologically active, i.e. those treatments that are applied in the middle of summer and winter respectively. A sexennial treatment was also included to determine the effect of infrequent but intense fires on the structure of marula.

The number of marula individuals in the lower canopy (trees and shrubs <2 m in height) were recorded in eight belt transects with a width of 10 m over the length of each plot. To ascertain the effect of fire on the structure of marula trees in the lower canopy, the height, crown and basal diameters of these individuals were recorded. Where multi-stemmed individuals were encountered, the widest part of the basal diameter was recorded. The stem status of the individuals in the lower canopy, being either multi- (M) or single- (S) stemmed, was also noted to determine the number of coppicing marula trees as opposed to single-stemmed individuals.

The mature marula trees (woody plants >2 m with one or a few definite trunks branching above ground level, as defined by Edwards (1983)) in the above treatments were also recorded. The girth at breast height (GBH) and the height of each tree were measured. If the girth could not be measured because of elephant damage, or because the trunk forked below breast height, the girth at ground level was measured. The regression fitted by Haig (1999) with $r^2 = 0.967$ ($p<0.001$) of age on basal circumference of marula was used to derive the approximate age of the trees occurring on the experimental burn plots. The marula growth form is such that there is not a great difference between the basal circumference and the circumference at breast height, thus it can be assumed that the derived age to be accurate when substituting basal diameter with GBH.

Unpublished field data gathered annually by Potgieter (1999)[2] were used to estimate mean fire intensities that occurred on the different treatments during the period 1987 to 1998. Fire intensity has only been recorded since 1987, and due to missing data, only values recorded for 1987 to 1992 and 1995 to 1998 were used to predict fire intensities to which the treatment blocks were subjected. Average fire intensities were estimated for each block, and classified into one of the categories proposed by Trollope & Potgieter (1985). The following fire behaviour model (Trollope 1999) was used to predict fire intensities to which the treatment blocks were subjected:

$$FI = 2729 + (0.8684\ x_1) - (530\ \sqrt{x_2}) - (0.1907\ x_3^{\ 2}) - (596\ 1/x_4)$$

Where:	FI	= fire intensity ($kJ.s^{-1}.m^{-1}$)
	x_1	= fuel load ($kg.ha^{-1}$)
	x_2	= fuel moisture (%)
	x_3	= relative humidity (%)
	x_4	= wind speed ($m.s^{-1}$)

Unpublished data (Trollope 1998)[1] were used to determine the height reduction response (100% (1 – height after burn/height before burn)) of marula trees across all height classes to different fire intensities, ranging from 110 $kJ.s^{-1}.m^{-1}$ to 6704 $kJ.s^{-1}.m^{-1}$. The fires applied to these blocks comprised the annual and biennial treatments during August and October 1989, and the biennial and triennial burning treatments applied during February 1987 (Trollope *et al.* 1995b). The responses of the various woody species were recorded in two transects laid down the center of each half of the plot, and approximately 20 survey points in each transect were taken. At each survey point the species, height and response of the nearest established tree or shrub were recorded in each quadrant (Trollope *et al.* 1995b).

[2] POTGIETER, A.L.F. 1999. Unpublished fire data recorded for the controlled burns applied on the Experimental Burn Plots in the *Sclerocarya birrea/ Acacia nigrescens* savanna in the Kruger National Park. Scientific Services, Kruger National Park, Skukuza.

Hlangwine Exclosure

Three blocks in the Hlangwine exclosure (permanently labeled C, B and E) were used to study the reaction of marula individuals to different burning treatments in the absence of herbivory. The burning treatments comprised burning in the middle of summer (C), late winter (E) and autumn (B). Before burning, 50 marula individuals (independent of height) were marked with metal markers, in each of these blocks. Variable numbers of belt transects of 10 m x 50 m were laid out in the different blocks until a total of 50 individuals had been recorded. The height, crown diameter and stem status (multi or single-stemmed) of these individuals were recorded before and after applying the controlled burns. The blocks had not been subjected to any specific burning treatments in the past, and therefore only the fire intensities of the different fires applied in this study were used in the analysis of the data (Table 9). The transects in block E burnt as a back fire, while those in blocks B and C burnt as head fires. Blocks B and E were re-sampled 6 months after the respective fire treatments (shortly after the vegetation started to coppice), while block C was re-sampled 2 months after the fire (as soon as the woody vegetation started to coppice).

The following parameters were recorded before and during the application of the burning treatments in the Hlangwine exclosure: fuel moisture, fuel load, size of burn, wind speed, air temperature and relative humidity, flame height and rate of spread. Values of 16 890 $kJ.kg^{-1}$ and 17781 $kJ.kg^{-1}$ were assumed as the heat yields for grass fuels burning as head and back fires, respectively. These data were used to estimate the intensity of the fires using the following equation (Trollope & Potgieter 1985): $I_H = y\, l\, r$

Where:
I_H = fire intensity ($kJ.s^{-1}.m^{-1}$)
y = heat yield ($kJ.kg^{-1}$)
l = fuel load ($kg.m^{-2}$)
r = rate of spread ($m.s^{-1}$)

Data analysis

Experimental Burn Plots.

Analysis of variance was used to examine the data that were normally distributed, i.e. the height, crown, log-transformed basal measurements and GBH measurements. The densities of marula trees in the lower canopy were found to be negative binomially distributed and were thus analysed using a negative binomial regression. The proportion of single-stemmed individuals in the lower canopy were examined using logistic regression analysis with over-dispersion corrected using the Williams procedure. Each response was initially examined across all treatments (A1, A2, A3, F2, F3 and XC) and then across a subset of the data (A2, A3 and F2, F3) for separate season and frequency effects. Extremely low counts on the Lindanda replicate and on certain treatments meant that the replicate by treatment interaction could not be estimated.

Table 9

Fire intensity category and fire type of the fire treatments applied to three study blocks in the Hlangwine exclosure.

Block	Season	Resample period	Fire type	Fire Intensity $KJ.s^{-1}.m^{-1}$	Fire Category
B	Autumn	6 months	Head	4851	Extremely hot
C	Mid-summer	2 months	Head	1381	Moderate
E	Late winter	6 months	Back	210	Very cool

Analysis of variance was further used to investigate the variation in fire intensity on the experimental burn plots. Non-linear regression analysis were used to determine the relationship between reduction and fire intensity as well as between reduction and height of marula individuals.

Hlangwine exclosure.

The data collected in the three blocks in the Hlangwine exclosure were pooled and an escape height determined. Changes in height and crown diameter after the lower canopy was exposed to different fire intensities were examined by means of analysis of variance. There was no option but to pseudo-replicate the experiment as the ecology and fire behaviour could not be replicated in the limited exclosures available. Linear regression analysis was used to determine the relationship between height and crown diameter for marula individuals in the lower canopy. A saturated logistic regression was used to determine the proportion of single-stemmed individuals that changed to multi-stemmed individuals after application of the burn treatments.

Results

Experimental Burn Plots

A summary of the observed responses of marula to fires is given in Figures 16 and 17, and each vegetation parameter discussed below. None significant effects are indicated as no response.

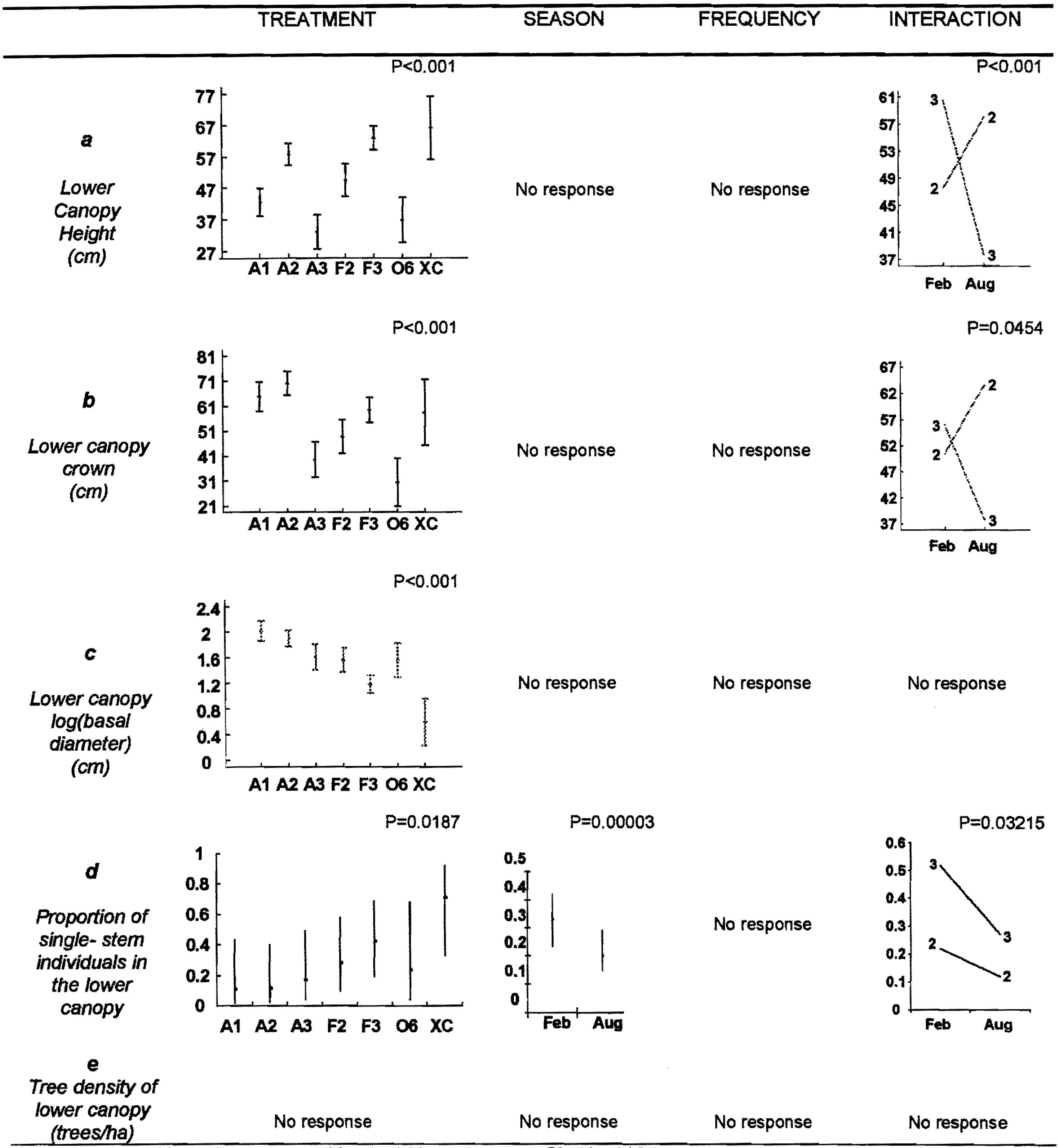
Lower canopy.

Height response.

Height differs significantly across replicates ($p<0.001$) and treatments (Figure 16a). Individuals in the lower canopy on Marheya were significantly taller (0.678 m; ± 3.896) than on the other replicates while those on Satara were significantly shorter (0.259 m; ± 9.260). Although the main effect of both season and frequency were not significant, the season by frequency interaction was significant (Figure 16a). Very few marula individuals between 1.5 m and 2 m were present, while the heights below 1.5 m were well represented.

Crown response.

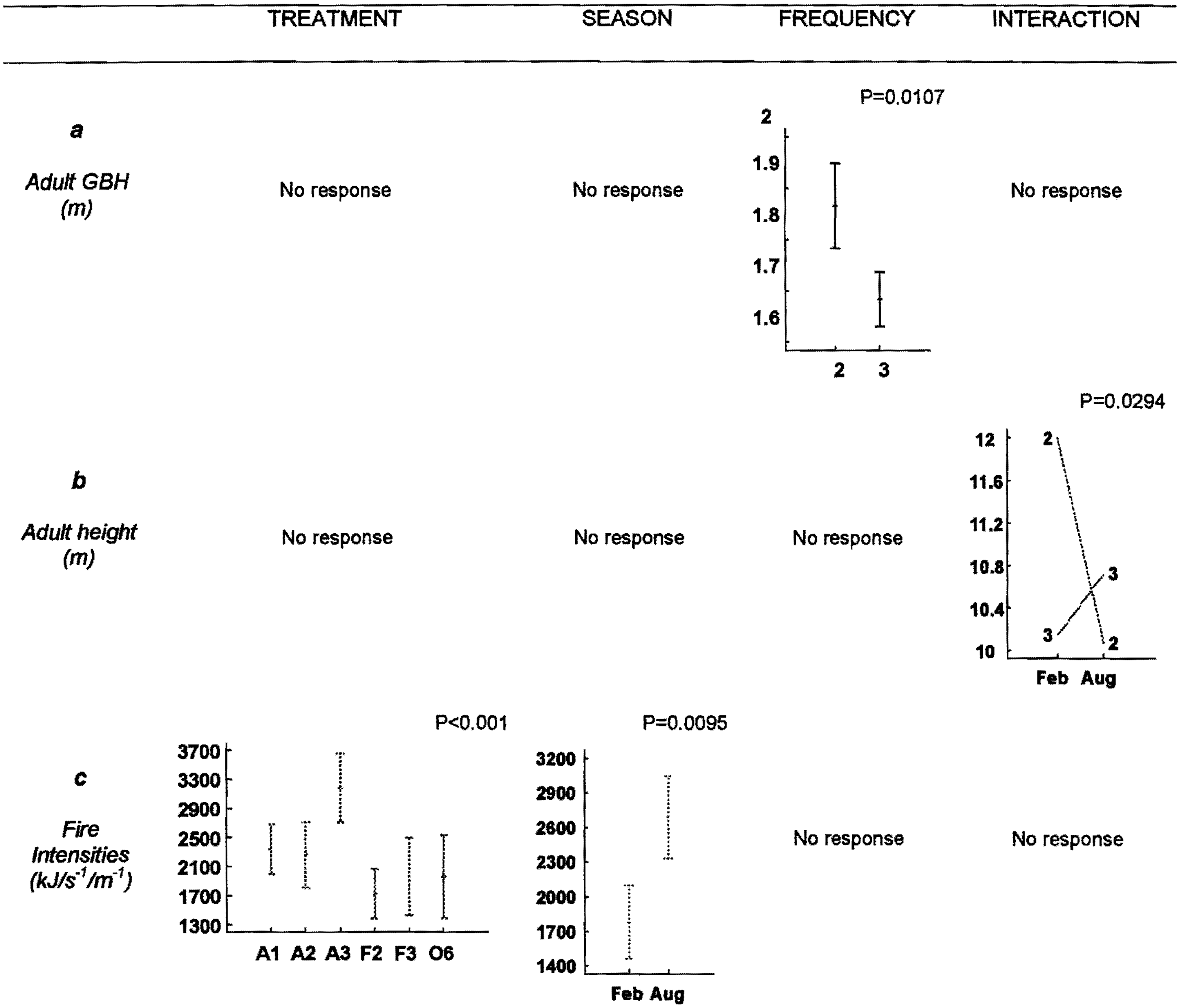
Crown diameter differed significantly across replicates ($p<0.001$) and treatments (Figure 16b). Only the interaction between frequency and season was significant (Figure 16b). Biennial and triennial February burns yielded very similar crown diameters, whereas biennial August burns yielded significantly wider crown diameters than the August triennial burns.



A1 – annual August burn A2 – biennial August burn A3 – triennial August burn F2 – biennial February burn F3 – triennial February burn O6 – sexennial October burn XC – Fire exclosure

- No response = not significant at p=0.05 * Bars represent 95% confidence intervals

Figure 16. Responses of *Sclerocarya birrea* individuals <2.75 m on the experimental burn plot trial in the *Sclerocarya birrea/Acacia nigrescens* savanna.



A1 – annual August burn
A2 – biennial August burn
A3 – triennial August burn
F2 – biennial February burn
F3 – triennial February burn
O6 – sexennial October burn
XC – Fire exclosure

* No response = not significant at p=0.05 * Bars represent 95% confidence intervals

Figure 17. Responses of *Sclerocarya birrea* individuals >2.75 m on the experimental burn plot trial in the *Sclerocarya birrea/Acacia nigrescens* savanna and fire intensities.

Basal diameter response.

The log-transformed basal diameter of individuals in the lower canopy differed significantly across replicates ($p<0.001$) and treatments (Figure 16c). The August annual burn yielded a wider basal diameter (8.16 cm) than all treatments except the August biennial burn, from which it did not differ significantly. The basal diameter of seedlings did not respond significantly to the main effects of season and frequency of burn, or to their interaction.

Proportion of single-stemmed individuals.

Internal contrast tests show that the fire exclosure (71%) had a significantly higher proportion of single-stemmed individuals than the August treatments, but did not differ significantly from the February and sexennial October treatments. Significant differences in the proportion of single-stemmed individuals were observed across treatments, but not replicates (Figure 16d). Examined for separate season and frequency effects revealed a significant season effect, as well as interactions between replicate and frequency, and between frequency and season (Figure 16d).

Tree density of lower canopy.

A negative binomial regression analysis showed that there were no significant differences in density between treatments, replicates or their interaction. The minimum adequate model was constant plus treatment which explained 35.26% of the total deviance. Examined for separate season and frequency effects also yielded no significant differences between seasons, frequencies, replicates or the interactions of these parameters (Figure 16e).

Mature Trees.

Girth response.

The girth at breast height did not differ significantly across treatments ($p = 0.0799$) or replicates. The main effect of frequency was significant (Figure 17a).

Height response.

The effects of treatment and replicate on mature tree height were not significant, whereas the season by frequency interaction was significant (Figure 17b). The regression for height on GBH did not have a good fit ($r^2 = 0.1307$ and $p<0.001$). No mature trees between 2 m and 7 m tall were found on any of the treatments, including the fire exclosure. However, all the heights between 7 m and 14 m were well represented.

Fire intensities.

With year as a covariate ($p<0.001$), it is clear that fire intensities differed significantly across the different treatments, but not across replicates (Figure 17c). The main effect of season is significant (Figure 17c). Table 10 shows the fire intensities of the different treatments.

Table 10

The fire intensities ($kJ.s^{-1}.m^{-1}$) of the different treatments of the experimental burn plots used in this study.

Treatment	Mean	Maximum	Standard deviance	Fire category
August 1	2305	4203	289.24	Hot
August 2	2228	4606	1356.78	Hot
August 3	3144	4282	935.65	Extremely hot
February 2	1723	5302	1439.67	Moderate
February 3	1993	4370	1560.66	Moderate
October 6	2185	3729	827.34	Hot

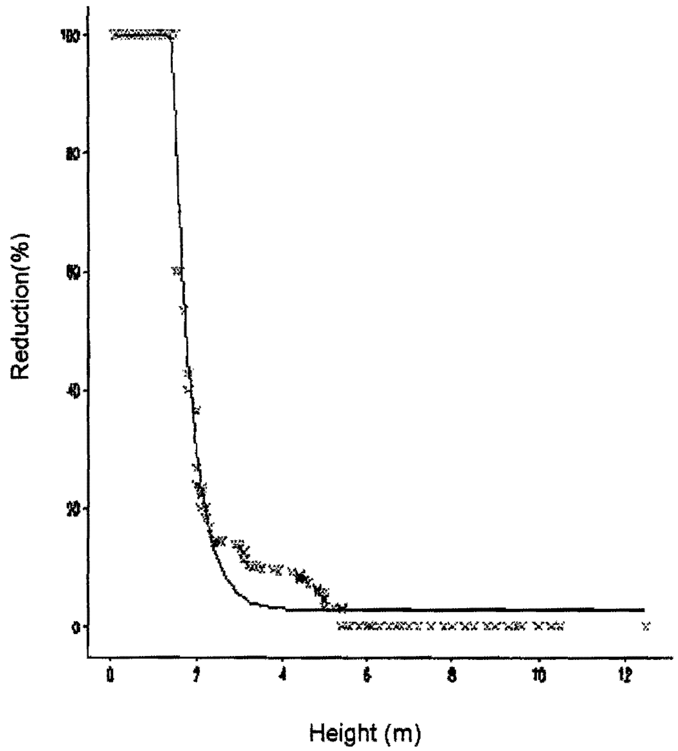
Reduction Response

A scatter plot of reduction plotted against fire intensity revealed no relationship between these parameters, and none of a wide range of curves could be fitted successfully to the data. A non-linear generalized logistic regression shows a very clear relationship between height and fire reduction ($p = <0.001$, $r^2 = 99.4\%$) (Figure 16). The following empirical equation can be used to predict reduction of *S. birrea* from height:

$$\text{Reduction (\%)} = 2.78 + \frac{97.24}{\{1 + 19 \exp[43.77 (\text{height} - 1.505)]\}^{1/19}} \quad \text{(m)}$$

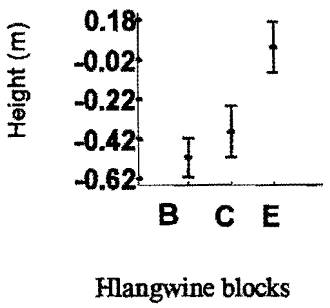
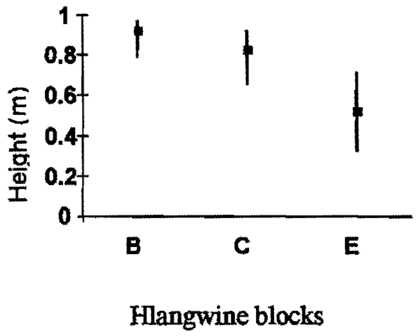
The Hlangwine Exclosure

The responses of *Sclerocarya birrea* to fire in the Hlangwine exclosure are depicted in Figure 18 and Figure 19.



——— Fitted line xxxxxx Observed line

Figure 18. Fitted versus observed relationship between height and reduction of *Sclerocarya birrea*.

a	*b*	*c*
Change in height for trees >2.75m (after – before burn)	Change in crown Response	Proportion of single-stemmed <2.75m to multi-stemmed after burn
P<0.001		P<0.001
	No response across the different blocks	

* No response = not significant at p=0.05   * Bars represent 95% Confidence Intervals

Figure 19. Responses of *Sclerocarya birrea* to fire in the Hlangwine exclosure.

Mortality response.

No marula individuals in the data set experienced mortality across the range of fire intensities recorded on the three blocks. The smallest marula seedling recorded (20 cm on block B) survived the extremely hot fire application by coppicing from the basal region.

Height response.

The tallest tree affected by fire was found to be 2.70 m (Figure 18). Only trees below the empirical fire escape height of 2.75 m were therefore, used to investigate the effect of fire on the structure of marula trees in the Hlangwine camp. The empirical escape heights of the three blocks did not differ significantly.

The change in height (height after burn – height before burn) differs significantly across different fire intensities (Figure 19a). The maximum reductions in height were B = - 2.2 m, C = - 1.9 m and

E = - 0.43 m. The maximum regrowth measured for the different blocks were B = 0.15 m, C = 0.3 m and E = 0.6 m.

Crown response.

Although the change in crown diameter did not differ significantly across the different blocks, a t-test used on the pooled data revealed an overall average decrease of 10.89 cm ($p = 0.003$) on the three blocks.

A linear regression analysis shows a positive correlation between height and crown diameter ($p<0.001$, $r^2 = 59.1\%$). The relationship between height and crown remained very similar before and after the burn; the relationship before the burn being given by the equation: crown = 0.1778 + 0.16163 x (height <2.75).

Single versus Multi-stemmed.

The proportion of single-stemmed individuals which changed to multi-stemmed after fire application, differed significantly across the three blocks (Figure 19c), and block E differed significantly from blocks B and C.

Discussion

The Experimental Burn Plots

Lower canopy.

Height and crown response.

Height and crown diameter of the lower canopy was significantly affected by the interaction between season and frequency, but not by the main effects of these parameters (Figure 16a & b). This corresponds with results of Trollope *et al.* (1998b) who found that vegetation in the Kruger National Park is not sensitive to the season of burn. However, these results contradict Trollope *et al.* (1998b) who suggested that the frequency of fire has a highly significant impact on woody phytomass.

Height and crown responses displayed similar trends (Figure 16a & b). Individuals in the lower canopy on the biennial August treatments were taller than those on the other August treatments, suggesting favourable conditions for reaching a fire escape height. Compared to those on the annual August treatments, they have a one-year longer fire return period in which to grow taller. By the August triennial treatments, fuel accumulation results in extremely hot fires, which negate further gains in height. Although annual August fires have significantly lower fire intensities (hot) than August triennial burns, the annual fire return period prevents the individuals in the lower canopy from developing into taller ones. Annual burns also attract increased herbivory, especially from *Aepyceros melampus* (impala) and *Equus burchellii* (zebra) (E.D. Salvesen & M.A.J. Eschenlohr, In prep. 2000), and this may result in increased browsing on woody vegetation. The triennial February burns have a combination of a longer fire return period and moderate fire intensity, resulting in a taller marula structure (Figure 16a). As expected, the exclusion of fire on the fire exclosure plots yielded tall seedlings due to the lack of topkill (Figure 16a). However, the height of individuals in the lower canopy on the fire exclosure is probably suppressed by competition from the herbaceous layer that has not burnt since 1954, resulting in the average height not being much higher than on the other treatments.

Individuals in the lower canopy exposed to the biennial August burns appear to have a bigger structure (height and crown) than seedlings on the biennial February treatments (Figure 16a & b). This is most probably due to the physiological state of the seedlings when exposed to frequent summer burns as opposed to frequent winter burns. The fact that seedlings on the Marheya replicate have the largest structure in terms of height, crown and basal diameter, whereas those on the Satara replicate have the smallest structure (height and crown), can probably be ascribed to finer scale variation in soils and herbivory pressure within the *Sclerocarya birrea/Acacia nigrescens* landscape.

It is interesting to note that the individuals in the lower canopy of the triennial February burn (half of which became the sexennial October treatment in 1979) differed significantly in height and crown diameter from the sexennial October burn, even though the sexennial October burn has only been subjected to three burns since initiation (Figure 16a & b). Due to this relatively short treatment period, the sexennial October treatment may not be a true reflection of long term marula response to sexennial summer burns. Only individuals in the lower canopy on the sexennial October treatment differed significantly from the fire exclosure in both height and crown diameter, suggesting that this treatment may result in dramatic long-term structural changes.

The differences in the mean basal diameter of individuals in the lower canopy across treatments (Figure 16c) and replicates correspond with the differences in the mean basal diameter of all woody vegetation as found by Enslin *et al.* (2000). As expected, the mean basal diameter of the fire exclosure was significantly smaller than that of all other treatments. Once marula individuals in the lower canopy are exposed to fire (independent of treatment), they coppice from the collar region at the base of the plants, resulting in a significant increase in the basal diameter as well as the proportion of multi-stemmed individuals (Figure 16c & d). This corresponds with results of Trollope *et al.* (1995b), who found that 63% of all woody vegetation sampled, coppiced from the collar region after being subjected to a range of fire intensities.

The higher proportion of single-stemmed individuals in the February treatments and fire exclosure as opposed to the August treatments (Figure 16d), can be explained by the significantly higher fire intensities in August, which result in greater basal coppicing. Higher herbivory pressure on the annual August burns probably contributed to the low proportion of single-stemmed individuals. The presence of multi-stemmed individuals on the fire exclosure plots can only be attributed to herbivory effects.

Examining the density results of the lower canopy across treatments, it is clear that fire does not have a significant impact on the density of marula individuals (Figure 16e). This corresponds with results of Enslin *et al.* (2000), who found that the total woody species diversity and composition on the experimental burn plots did not change between 1954 and 1998, and specifically found no significant marula tree density changes in this landscape. The results also support Trollope *et al.* (1998a) who stated that the frequency of burning does not have a significant effect on the density of woody plants.

Mature trees.

By deriving the age of mature trees from GBH measurements (Haig 1999), it appears that all surveyed trees are at least 80 years old. These results, indicate that no mature trees have become established on the experimental burn plots during the past 80 years. This could possibly be ascribed to unfavourable conditions for recruitment of lower canopy marula individuals into the mature population during the 34 years prior to the start of the trial, or perhaps thereafter. Should favourable conditions for marula recruitment have arisen since the start of the trial, the effects of fire and herbivory on the surveyed plots during the past 46 years may have prevented marula individuals from reaching the fire escape height, and could possibly have resulted in the mortality of trees which were just above the empirical escape height at the time the trial was initiated.

Examining the GBH of these adult marula individuals, it seems that longer fire return periods (triennial burns) resulted in smaller GBH than shorter fire return periods (biennial burns), which cause more frequent topkill (Figure 17a). It appears as if the height of mature trees is not much affected by fire, which can be expected as such individuals have outgrown the fire sensitive height (2.5 to 3 m). However, there is a height response to the season by frequency interaction. The conclusion of the GBH and height results indicate that long-term fire treatments can perhaps have an effect on adult marula trees.

Reduction Response

Examining the height reduction response of marula, there is no relationship between reduction and fire intensity. This contradicts the results found for individuals in the lower canopy on the experimental burn plot trial, but can be explained by the fact that the lower canopy as well as adult trees, which differ in their response to fire, were included in this reduction study.

The highly significant regression of fire reduction on height is evidence of the overriding influence of height on susceptibility of plants to fire (Figure 20). These results further provide an independent verification of an empirical escape height between 2.5 and 3.0 m for marula. The threshold at 1.5 m suggests that marula seedlings are particularly susceptible to fire, as this height is substantially greater than the height of 0.5 m determined by Trollope (1983) as being the height below which shrubs and seedlings in general suffer significant topkill, irrespective of fire intensity.

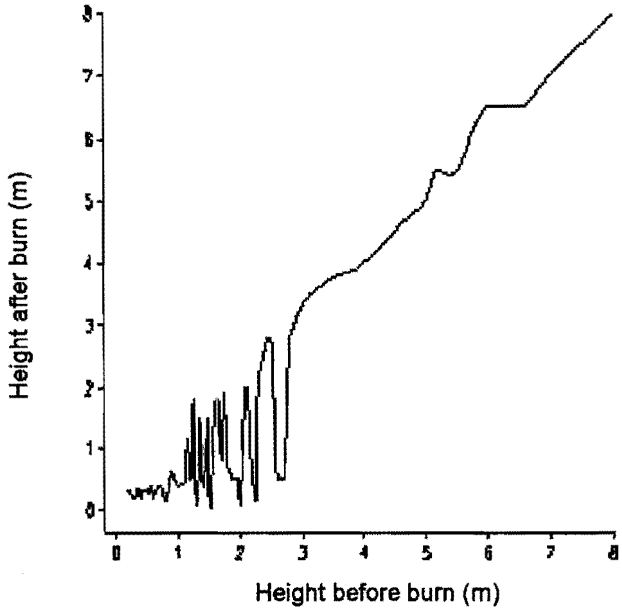


Figure 20. Line plot of height after burn against height before burn for *Sclerocarya birrea* individuals in the Hlangwine exclosure.

The Hlangwine Exclosure

No mortality and hence no density changes occurred in the study conducted in the Hlangwine exclosure. This supports the results obtained from the experimental burn plot trial in this study as well as Enslin *et al.* (2000).

Examining the response of height and crown diameter of marula individuals <2.75 m tall, it appears that differing fire intensities only have significantly different effects on the height structure. Although burning results in a decrease in crown diameter, this decrease does not differ significantly for different fire intensities. Very cool fires do not have a significant impact on height, whereas moderate to extremely hot fires result in significant decreases in height. This corresponds with Trollope *et al.* (1998b), who found that a 2 500 kJ. $s^{-1}.m^{-1}$ fire intensity has a significant effect on height structure, as it results in 53.2% topkill of bush.

Examining the height regrowth response, the least regrowth was found to appear on the extremely hot April burn (block B). This corresponds with Enslin *et al.* (2000) who found that the woody layer is at a physiologically sensitive state (at a growth peak) at this time of year, and is therefore more vulnerable to coppicing and hence regrowth. Marula individuals <2.75 m appear to recover to their initial height and crown structure within six months of being subjected to a very cool fire in late winter. Although the reduction in height between blocks B (extremely hot) and C (moderate) is not significantly different, the marula individuals of block C have recovered much faster as coppicing already took place two months after being burnt. The regrowth at this time was already twice as much as on block B that was re-measured 6 months after the burn. This supports Trollope *et al.* (1998b), who suggested that fires should be applied when vegetation is normally physiologically dormant (mid winter) and physiologically active (mid summer), and not during their sensitive physiological state (autumn and spring).

Similar trends to the experimental burn plot results were found when examining the proportion of single-stemmed, where all three blocks yielded a significant change to a multi-stemmed morphology after being burnt. It appears that there is a correlation between fire intensity and change in morphology, where increased fire intensities yield a greater change to the multi-stemmed morphology.

Conclusions

The variance in seasonality and frequency resulted in different effects of fire on marula. Bailey (1995) also found the effect of fire to be variable and contradictory depending on rangeland ecosystem and circumstances. Results of this study further support Bailey (1988) in stating that response of vegetation to fire depends upon frequency, seasonality and intensity, but showed that the interaction between the main effects of season and frequency was the incremental factor. The changes in the woody vegetation in response to fire did not involve a decrease in species diversity, but rather a change in vegetation structure and morphology, and support those of Trollope *et al.* (1995b), Enslin *et al.* (2000) and Bailey (1988) who stated that repeated burning often increases the species diversity. Results also support Sweet (1982) who found that fire did not significantly affect the density of trees or shrubs, but it affected the structure of the woody vegetation.

Marula seedlings up to a height of 1.5 m are particularly susceptible to fire, and they generally respond to the frequency by season interaction, and not to the main effects of season or frequency. However, results support Trollope *et al.* (1998b) in suggesting that management fires are best applied during mid-summer or mid-winter. Fire enhances the change in the structure of marula seedlings to multi-stemmed, where increased fire intensity results in increased proportions of multi-stemmed individuals. As opposed to the individuals in the lower canopy, adult trees do not respond to fire. Results show the empirical escape height for marulas to be between 2.5 and 3.0 m.

The triennial August burns appear to have the greatest impact on the marula seedlings, probably due to the extremely high fire intensities resulting in increased topkill. The annual August treatments seem to attract increased herbivory, resulting in this treatment having height and basal diameter responses similar to the triennial August treatment. The February treatments and biennial August burn seems to have the least impact on the structure of marula seedlings, indicating favourable conditions for reaching a fire escape height.

Between 1954 and 1992 the fire management policy of the Kruger National Park was to apply triennial burns during late winter on a rotational basis to the fire management blocks of the park (Trollope *et al.* 1998b). The extremely high fire intensities, with the resultant low heights and crown diameters recorded on the August triennial treatments in this study, strongly suggest that this burning policy has hampered the establishment and development of marula seedlings in the park. This may largely explain the observed lack of marula recruitment in the park over the past eighteen years. This supports the results of Enslin *et al.* (2000) who found that the woody vegetation is being transformed into a lower woodland community interspersed with a low density of large trees, together with significant changes in the proportion of single-stemmed individuals. This phenomenon should, however, not be viewed in isolation, as fire/herbivory interactions most probably contributed towards change in habitat.

The current *laissez faire* burning policy was introduced in 1994 where only fires ignited by lightning are permitted to burn and all other ignition sources are controlled as far as possible (Trollope *et al*. 1995a). Lightning ignited fires usually occur in summer with a shorter fire return period. Thus, the current policy may provide more favourable conditions under which marulas can reach less vulnerable heights (taller than 1.5 m). This change in fire policy may result in a turnaround in the observed adult marula decline in the Kruger National Park.

It is believed that some of the parameters and responses determined in this study can be useful for the modeling and understanding of savanna tree responses to fire. Areas of future research and monitoring highlighted by this study centre around the recruitment of lower canopy individuals into the adult population to ascertain whether the current fire policy provides favourable conditions for the establishment of adult marula trees. Although this study shows that fire does play a role in hampering recruitment, it is necessary to examine the population structure of marula in the rest of the *Sclerocarya birrea/Acacia nigrescens* savanna, in order to understand the role of fire in contrast to recruitment events.

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