EFFECT OF FIRE FREQUENCY ON HERBIVORE DISTRIBUTION AND BEHAVIOUR IN THE KRUGER NATIONAL PARK, SOUTH AFRICA

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Contents

Preface

The experimental work described in this dissertation was carried out in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, from January 2009 to December 2010, under the supervision of Professor Kevin Kirkman and co-supervised by Dr Nicole Hagenah (UKZN) and Professor Melinda Smith (Yale University). These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others it is duly acknowledged in the text.

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Declaration 1 – Plagiarism

I, Sindiso Charlotte Chamane, declare that

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Format used in thesis:

This thesis has been prepared as a series of two results chapters formatted as papers, with chapter 1 giving a brief general introduction with motivation and research questions for the study, literature review and the description of the study site and the experimental set-up. Chapter 4 gives a brief conclusion highlighting the main findings of the work and recommendations for further studies. Chapter 2 – 3 are the results chapters formatted as papers, note that the all figures and tables are placed at the end of the thesis. Note that the experimental set-up was only explained in detail in chapter one to avoid repetition in the thesis.

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Abstract

Fire plays an important role in structuring and maintaining savanna grassland ecosystems. Although regular fires are a characteristic feature of savannas, the effects of fire frequency on these systems are less well known, particularly with respect to how frequency of fire influences large herbivore distribution and behaviour. The expectation is that large herbivores should be attracted to frequently burned sites as a consequence of changes in forage quality and quantity, and/or vegetation structure and composition. The former could be driven by alterations in soil nutrients, such as N and P. Alterations in vegetation also could be important in determining risk of predation. For example, an increase in woody vegetation could decrease predator visibility making large herbivores more vulnerable to predation. The objectives of this study were to investigate the effects of long-term alterations in fire frequency on herbivore distribution and behaviour, as well as the mechanisms (soil nutrients, vegetation structure and composition, and forage quality and quantity) potentially driving the distribution of large herbivores. To address these objectives, I conducted large herbivore surveys on a bi-weekly basis from 2009-2010 in a series of plots in the Experimental Burn Plots (EBPs) burnt at different frequencies (annual, triennial and unburnt) over the last five decades at three study sites in the Kruger National Park, South Africa. Surveys also were conducted on new plots that were established adjacent to the long-term plots. These new plots have a fire return interval of 4 years which is similar to the triennially burned plots of the EBPs. They were established in the landscape adjacent to the EBPs to assess whether the responses of herbivores to fire observed in the EBPs reflected was at landscape level.

The distribution of all large herbivore species combined and of grazers (e.g. zebra) or browsers (e.g. kudu) only were not affected by fire frequency. In contrast, the abundance of

mixed-feeders, such as impala, was significantly higher in the unburnt (control) and annually burned plots than the triennially burned plots. Although season did not have a significant impact on the distribution of browsers and mixed-feeders, overall more grazers were recorded across all burn treatments in the dry season compared to the wet season. Similar patterns of herbivore distribution were observed between the new plots and the triennially burned EBP plots, suggesting that responses observed to the long-term fire frequency treatments reflects herbivore responses at the landscape level. The long-term fire frequency treatments significantly affected soil nutrients (N, organic C, P, and K were significantly lower with annual burning), vegetation structure (abundance of woody plants were greater in unburned plots), and forage quantity (unburned plots had higher biomass) but not quality. More frequent fires improved visibility by reducing tree height and density and herbaceous biomass, thereby potentially reducing predation risk, when compared to less frequent burning. As a result, herbivores selected sites with more frequent fires. The behaviour of the herbivore species investigated was predominantly influenced by seasonal-induced changes to their environment rather than fire frequency. In the wet season irrespective of the burning treatment visibility was low due to high rainfall that increases plant biomass, whereas in the dry season visibility was improved because there is little to no rainfall. This potential alteration in predation risk likely resulted in herbivores being more vigilant in the wet season than the dry season. Overall, results from this study suggest that the combination of fire frequency and season drive herbivore distribution and behaviour by altering mainly the vegetation structure which can influence predation risk.

Chapter 1

General introduction

Fire has played a central role in shaping and maintaining the structure and function of fire-prone plant communities (Bird and Cali, 1998; Bond and Keeley, 2005). Savannas and C4 grasslands, especially in more humid regions such as the wetter regions of Africa, are the most frequently burnt ecosystems in the world because they provide favourable conditions for fires (Bond and Keeley, 2005). Past or future changes in the extent of these ecosystems, or species within them, cannot be understood without understanding the ecology of fire (Bond and Keeley, 2005). Studies in different regions of the globe have been carried out on the ecology of fire (Payne, 1995; Bird and Cali, 1998). However despite many years of research, the issue of how to manage fires and fire regimes in conservation areas is still the subject of debate.

In African savanna ecosystems, active fire management has been practiced for many decades and policies and practices have changed as new evidence on the role of fire has emerged (Bond and Archibald, 2003). The Kruger National Park in South Africa has a long history of fire management (Van Wilgen et al., 2004) and fire experimentation (Biggs et al., 2003). Research has shown that the interaction between fire and herbivores shapes savanna grassland ecosystems (Hobbs et al., 1991; Scholes and Archer, 1997; Liedloff et al., 2001; Van Langevelde et al., 2003). Although the effects of fire and herbivory on vegetation are well documented (Bond and Van Wilgen, 1996; Uys et al., 2004), the effect of fire, particularly fire frequency, on herbivore distribution and behaviour is less well known. To better understand the plant community and ecosystem responses to fire and herbivory, it is critical to examine how herbivores respond to fire regimes and the mechanisms underlying these responses.

This study addressed the effects of fire frequency on the distribution and behaviour of large (> 5kg) mammalian herbivores in selected Experimental Burn Plots (EBPs) with varying fire frequencies at Satara, Marheya and N'wanetsi in the central Kruger National Park, and the underlying mechanisms driving both herbivore distribution and behaviour. The possible driving mechanisms that were investigated were soil nutrients, forage quality, forage quantity, visibility measurements to assess predation risks, and vegetation structure and plant species composition. The specific objectives were to determine:

1. The effects of fire frequency on soil nutrients and vegetation structure, plant species composition and seasonal changes in plant quality (measured as digestibility and C:N ratio for the dominant grass species) and standing plant biomass;
2. The effects of fire frequency on seasonal distribution of large (> 5kg) mammalian herbivores by conducting dung counts (as an indication of herbivore presence) and herbivore diurnal and nocturnal surveys;
3. The relationship between the effects of fire frequency on vegetation and herbivore distribution; and
4. The effects of fire frequency on seasonal behaviour of mammalian herbivores i.e. to determine the activities they engage in during the day and the time taken up by those activities.

Literature review

Fire in African savannas

Savannas are characterized by the coexistence of trees and grasses and occupy about one fifth of the earth's surface (Van Wilgen et al., 2000). Savannas support a large portion of the world's human population and livestock, rangeland and wild herbivore biomass (Sankaran et al., 2005). Fire has historically played and continues to play an important role in shaping savanna ecosystems. The role of fire on savanna ecosystems became more prominent due to anthropogenic activities (Bond and Van Wilgen, 1996). With the introduction of agriculture and pastoralism in African savanna ecosystems ca. 5000 years ago, the frequency of anthropogenic fires has significantly increased (Bond and Van Wilgen, 1996). Fire was used to clear land for cultivation, to reduce bush encroachment and to remove old plant material, thus creating space for new plant growth (Oluwole et al., 2008). Ultimately, these burning practices resulted in the reduction of forested areas and an increase of more open savannas (Van de Vijver et al., 1999).

Effect of fire on soil and vegetation

Soil

Fire affects the soil directly by temporarily increasing soil temperatures and indirectly by modifying the activity of the soil biota (Frost and Robertson, 1987). Fires also reduce plant biomass and litter, thereby changing energy, nutrient and water fluxes between the soil, plants and atmosphere (Cass et al., 1984; Frost and Robertson, 1987). Fire has beneficial and non-beneficial effects on nutrient availability in soils i.e. fire releases nutrients into the soil from dead plant matter, but also volatilizes nutrients into the atmosphere (Fynn et al., 2003). Also, nutrients rapidly released by fire into the soil are prone to loss through leaching whereas nutrients slowly released through decomposition of plant matter are not readily lost through leaching (Fynn et al., 2003).

Vegetation

The effect of fire on plant community structure and composition is highly variable and these effects are often dependent on a number of factors such as soil moisture, altitude, and the vegetative and reproductive traits of the plant species present (Wardell-Johnson and Horwitz, 2000). Fire frequency determines the length of time that a plant has to recover before the next fire occurs (Frost and Robertson, 1987; Andersen et al., 2005). The slower the rate of recovery, the more likely it is that the structure and composition of the vegetation will be altered, particularly where fire occurs frequently (Frost and Robertson, 1987; Van Wilgen et al., 2003). Plant species which are tolerant of fire and regenerate vegetatively generally recover faster than species which only regenerate from seed (Higgins et al., 2007). Plant species regenerating from seeds must establish, grow and reproduce in the interval between successive fires in order to survive recurrent fires (Sankaran et al., 2005). The high fire frequency in savannas is one of the main factors selecting against such species, particularly among woody plants. As a result, frequent fire reduces woody plant densities in savannas (Boultwood and Rodel, 1981; Mapiye et al., 2008; Smit et al., 2010).

Effect of fire on herbivores

The effects of fire on herbivores can be direct or indirect. However, large mammalian herbivores are less likely to be affected by the direct effect of fire because they can escape a fire. The direct effect of fire refers to burning of animals. It has been suggested that large mammalian herbivores are mostly affected by the indirect impacts of fire (Mapiye et al., 2008). Indirect effects of fire are related to the alteration of the physical environment. Fire alters vegetation structure and composition, and can result in changes in resource availability for herbivores, mainly grazing herbivores (Mills and Fey, 2005). This can lead to changes in the quality and quantity of herbivore forage. Shortly after a burn, the nutritional quality of forage is high while forage quantity is relatively low (Gujera and Owen-Smith, 2002). Animals prefer these burnt areas because of the increased forage protein, palatability and digestibility (Fuhlendorf and Engle, 2004; Mapiye et al., 2008). Another indirect effect of fire is that herbivores may utilize the burned open areas because of the reduced predation risk due to the improved visibility (Owen-Smith, 2008).

Herbivore seasonal distributions and behaviour

The distribution and abundance of large mammalian herbivores is influenced by a number of factors namely (i) the presence of acceptable forage, (ii) the cover available to predators (iii) distance to water and (iv) the mobility of the herd (Funston et al., 1994; McNaughton et al., 1997). During the wet season when food is abundant, group-living mammalian herbivores, such as buffalo, form large herds. Forming large herds in the wet season is an advantage because it decreases predation risk in the high vegetation due to the dilution effects (Fryxell, 1990). In the dry season, when food sources are scarce, herbivores form small groups in order to move greater distances in search for food. Also, due to the lack of high vegetation in the dry season, these herds are able to spot predators from a greater distance (Bergstrom and Skarpe, 1999). Herbivores also use large areas in the wet season because surface water is freely available. During the dry season, they concentrate on areas with permanent water sources (Sinclair, 1977). Foraging behaviour varies between and within seasons for different species depending on their feeding guild and physiology (McNaughton, 1990). Below, the habitat preferences and the feeding ecology of browsing (e.g. kudu), mixed-feeding (e.g. impala) and grazing (e.g. zebra) feeding guilds for large mammalian herbivores are briefly described.

Browsers

Browsing mammalian herbivores predominantly browse, with a ratio of grass:browse in their diet being 15:85 (Furstenburg, 2005). Habitat selection for browsers is generally governed by the presence of acceptable density and high diversity of edible woody plants and a suitable tree density for cover (Owen-Smith, 1994; Furstenburg, 2005). Studies on the diet selection by browsers have shown seasonal changes (Owen-Smith and Cooper, 1989; Owen-Smith, 1994; Furstenburg, 2005). In the wet season, browsers feed on palatable deciduous woody plants and soft-stemmed forbs. In the dry season, they generally feed on wild fruits or seed pods. During the critical transition period in the late dry season, woody plants that produce leaves ahead of the first rains are consumed.

Mixed-feeders

Mixed-feeders browse as much as they graze, whether they browse or graze is generally affected by seasonal changes in food availability (Babaasa, 2000). In the wet season, they spend most of the time grazing and relatively little time browsing. In the dry season, grazing time drops and browsing time increases (Guy, 1976; Beekman and Prins, 1989; Rugiero, 1992; Kabigumila, 1993). This seasonal shift in diet is due to the changes in food quality. Mixed-feeders browse more during the dry season because crude protein content of browse is higher than that of grass (Barnes, 1982). Furthermore, grass tends to accumulate tannins and become more fibrous thus reducing its palatability during the dry season (Babaasa, 2000).

Grazers

Grazing mammalian herbivores predominantly graze (Owen-Smith, 1988; Prins, 1996). They prefer open savannas with sufficient palatable grasses (Perrin and Brereton-Stiles, 1999) and avoid grass species with a high content of secondary plant compounds such as tannins (Owen-Smith, 1988). During the wet season, food resources are abundant and forage quality is high thus grazers spend most of their time feeding (Du Toit, 2005). In the dry season, when food resources are scarce, grazers spend a lot of time selecting suitable patches of vegetation (Du Toit, 2005). The animals also include more low quality material to maximize food quantity during the dry season (Perrin and Brereton-Stiles, 1999).

Description of study site and experimental set-up

The Kruger National Park (KNP) in South Africa covers nearly 2 million hectares of land, and is the largest national park in the country. The study was conducted in the central region of the KNP. The mean annual rainfall in the central region of the Park is ca 500 mm, with most of the rains falling mainly between November and March. Soils are nutrient rich, derived from basalt parent material and have high clay levels (Mills and Fey, 2005). The vegetation is open, co-dominated by a variety of grasses including *Themeda triandra*, *Urochloa mosambicensis*, *Bothriochloa radicans* and *Digitaria eriantha* and trees consisting of *Acacia nigrescens* and *Sclerocarya birrea*. KNP is a home to a diverse group of large herbivores such as African elephant (*Loxodonta africana*), white rhinoceros (*Ceratotherium simum*), giraffe (*Giraffa camelopardalis*), cape buffalo (*Syncerus caffer*), Burchell's zebra (*Equus burchelli*), waterbuck (*Kobus ellipsiprymnus*), blue wildebeest (*Connochaetes taurinus*), kudu (*Tragelaphus strepsiceros*), warthog (*Phacochoerus aethiopicus*), impala (*Aepyceros melampus*), grey duiker

(*Sylvicarpa grimmia*) and steenbok (*Raphicerus campestris*). Large predators include lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatis*), wild dog (*Lycaon pictus*) and jackal (*Canis mesomelas*).

Kruger National Park has a long history of fire management and fire experimentation including the Experimental Burn Plots (EBPs) (Van Wilgen et al., 2004). The EBPs were established in 1954 with 12-14 different fire treatments in various areas of the park to assess the effects of different fire frequencies (one-, two-, three-, four- and six-year fire return intervals) and season of burning (spring, summer, autumn, and winter) on savanna vegetation (Biggs et al., 2003). Unburned control plots are included at all sites. These treatments have been applied to 7 ha rectangular plots separated from the surrounding vegetation by 4 to 5 m firebreaks (Biggs et al., 2003). They form a useful long term experimental platform for examining the interactions between fire and herbivores.

The study was carried out at three study sites with Experimental Burn Plots (EBPs) (Satara, N'wanetsi and Marheya), in the central region of the Park. The season of burn for the plots that were selected is winter (August). Each of the three study sites consisted of three 7-ha plots burned at different fire frequencies in the winter (August): annually burnt, triennially burnt, and unburnt (control) (Table 1 in Appendix B). The argument is often made that because of the relatively small size of the EBPs, herbivores concentrating on recently burnt plots may have a confounding effect on the response of herbivores to the different fire regimes, and this confounding effect is likely to be reflected in vegetation species composition. As a result, the EBPs may not be representative of the much larger areas with similar fire regimes. In an attempt to account for this, additional plots (hereafter referred to as "new plots") of approximately the same size and dimensions as the EBPs were established adjacent to the existing EBPs at each of the three sites. The mean fire interval of the adjacent areas containing the new plots was ~every 4 years (similar to the triennially burned plot on the EBPs). Thus, a total of 12 plots were used for the study (3 study sites x 4 fire treatments). All the plots were burned in 2009 (the year of this study) except for the unburnt plots. The distance of each plot to the nearest permanent water source ranged from 2 to 5 km. Large herbivores were not excluded from the plots, thus fire frequency effects represent the combined effects of fire and herbivory.

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Chapter 2: The effect of fire frequency on soil nutrients and vegetation characteristics in a South African semi-arid savanna

Abstract

Fire plays an important role in structuring and maintaining savanna grasslands ecosystems. Regular fires are one of the characteristic features of tropical savannas. This study examined the effect of fire frequency on soil nutrients, herbaceous biomass and quality, and vegetation structure and composition in plots burnt over the long-term (>50 years) at different frequencies (annual, triennial and unburned) located at three study sites in the Kruger National Park, South Africa. In addition, plots (hereafter referred to as "new plots") were established in the landscape adjacent to the experimental plots at each study site. These areas experienced a mean fire return interval of every four years at each study site. These new plots were established to assess if the experimental plots do reflect the larger landscape. Soil samples were collected from the plots once based on the assumption that soil chemistry does not vary appreciably over time and herbaceous vegetation (biomass, grass and forb basal cover, tree density, forage quality) was sampled monthly. Soil N, organic C, P and K were higher in the unburned (control) plot than in the other burning treatments. The levels of soil Mg and Ca were not affected by fire frequency. Fire frequency had an effect on herbaceous biomass, where the unburned plot had higher biomass than the burning treatments. Neither grass quality (C:N ratios) or plant species composition was affected by fire frequency. Although forb basal cover was not affected by fire frequency, grass basal cover, tree height, and tree density strongly decreased with increasing fire frequencies. Therefore, the effect of fire frequency is more pronounced on the structure of vegetation rather than the composition, with more frequent fires reducing the structure of vegetation thus creating open savannas. As a result fire frequency can be used as tool to create

open or closed savannas. The new plot showed similar results to the triennial burn on the EBPs for all the characteristics tested. Therefore the EBPs do reflect the larger landscape.

Introduction

Fire plays an important role in the development and maintenance of a savanna community (Trollope, 1982). Regular fires are one of the characteristic features of savannas (Frost and Robertson, 1987). Fire has been shown to release nutrients into the soil from dead plant matter (Mills and Fey, 2005). These nutrients are then taken up by plants. Herbivores access these nutrients either through the consumption of plants or via geophagy (Mills and Fey, 2005). Fire also causes changes in forage quality and quantity, shortly after a fire the forage quality is high but forage quantity is low (Gureja and Owen-Smith, 2002). Over the course of the growing season, however, the forage quality drops but forage quantity increases (Van Langevelde et al., 2003). However, the effects of fire frequency on savannas are poorly understood, particularly in terms of the interaction between fire and herbivorous animals (Mills and Fey, 2005). More specifically, little is known how fire frequency alters factors (e.g. soil nutrients, forage quantity and quality, vegetation composition and structure) that determine herbivore distribution and behaviour (Shackleton and Scholes, 2000, Higgins et al. 2007, Mapiye et al. 2008).

To study the effects of fire frequency and fire season on semi-arid savanna vegetation, the Experimental Burn Plots (EBPs) were established in 1954 in the Kruger National Park, South Africa (Biggs et al., 2003). The trials include various burning frequencies (annual, biennial, triennial, quadrennial and sexennial) which are applied in different seasons (autumn, winter, spring and summer), as well as protection from fire (unburned or control plot). The experiment is ongoing and has provided invaluable information on the role of fire in semi-arid savanna (Van

Wilgen et al., 2003). For example, fire frequency affected herbaceous plant communities by removing or reducing plant cover and litter but not the species composition (Van Wilgen et al., 2003). Fire frequency also had an effect on the structure of woody vegetation, but not on woody species composition. For example, in the frequently burnt plots (annually – triennially burnt) trees occurred at lower densities than in the unburned plots (Higgins et al., 2007).

Because the EBPs are relatively small, the impact of fire regimes observed in the plots may not reflect how similar fire regimes affect the surrounding areas where much larger areas are burnt. In an attempt to account for this, new plots of about the same size as the EBPs were created adjacent to the existing EBPs. The mean fire interval of the adjacent areas containing the new plots was ~4 years, but the scale of the fires was different historically, with the new plots being part of the surrounding landscape where fires generally burn over several hundred or thousand hectares. These scale differences are likely to influence the impact of herbivores on the burnt areas, with the relatively small EBP plots potentially being impacted to a greater degree by grazing and browsing than the surrounding landscape.

The aim of this study was to determine the effect of fire frequency, in the presence of large herbivores, on soil nutrients, herbaceous plant biomass and quality, and vegetation structure and composition on the selected EBPs (annual, triennial and unburned) and the new plots.

The key research questions addressed in this study were:

1. Are soil nutrients (nitrogen, organic carbon, phosphorus, potassium, magnesium and calcium) affected by different fire frequencies?

2. What is the impact of fire frequency on herbaceous biomass production and grass quality over time?
3. Are there differences in the plant species composition and woody plant structure between the various burning treatments?

Materials and methods

The study was carried out from July 2009 to June 2010 in the Experimental Burn Plots (EBPs) of the Kruger National Park (KNP), South Africa. The study included plots of three different fire treatments: annually burned, triennially burned, and a plot left unburned (control plots). In addition, plots (hereafter referred to as "new plots") were established in the landscape adjacent to the EBPs at each study site. These areas experienced a mean fire return interval of every four years at each study site. These new plots were established to assess if the experimental plots do reflect the larger landscape. Three study sites were selected, Satara, N'wanetsi and Marheya in the Satara region of the KNP. This resulted in a total of 12 plots (4 fire treatments x 3 study sites). All plots were burned in August 2009, except for the control plots.

Soil nutrients

In September 2009, five soil samples were collected per plot (after the fires but before the onset of the rains). As a result, 60 samples were collected (3 study sites x 4 fire treatments x 5 samples). Soil samples were collected only once based on the assumption that soil chemistry does not vary appreciably over time (Fynn et al., 2003). Samples were collected at 20 m intervals across the centre of the plot at a depth of 10 cm using a soil auger. Samples were analysed for total nitrogen, organic carbon, phosphorus, potassium, magnesium, and calcium, at the Soil Science Laboratory of the University of KwaZulu-Natal, South Africa.

Plant biomass (herbaceous)

Herbaceous plant standing biomass was measured using a standard disc pasture meter (1.5 kg metal disc, 45 cm in diameter) (Bransby and Tainton, 1977; Zambatis et al., 2006). In each plot, 200 measurements per month (January 2010 – June 2010) were taken systematically throughout each plot, with locations of each measurement at least 3 m apart to ensure independence. Additionally, different starting points for the measurements were selected for each survey, to ensure data independence over time. No measurements were taken shortly after the plots were burned (August – November 2009) due to the lack of plant biomass before the onset of the rains. Existing calibration equations developed by Zambatis et al. (2006) for the Kruger National Park were used to convert disc pasture readings to estimates of standing biomass.

Forage quality

Forage quality was determined for the dominant grass species in each study plot (Appendix A) using two methods: 1) digestibility, estimated as cellulase dry matter disappearance (CDMD), and 2) leaf C:N ratio. For the CDMD analysis, 10 g of plant material of each grass species was collected by clipping tufts to ground level. For the C:N ratio analysis, 20 leaves per grass species were collected from each plot. Samples were collected on a monthly basis from December 2009 to June 2010. All samples were oven-dried at 60 ˚C for 48 hours and later milled, with 5 g and 2 g subsamples used for CDMD and C:N ratio analysis, respectively**.** The CDMD analysis was carried out at the Grassland Science laboratory of the University of KwaZulu-Natal. The C:N ratio analysis was carried out at the Chemistry laboratory of the University of KwaZulu-Natal.

Herbaceous species composition and structure (measured as basal cover)

Herbaceous (forb and grass) species composition data was collected in March 2010. The point-to-tuft-distance method was used to record the species composition in each plot (Cottam and Curtis, 1956; Hardy and Tainton, 1993). Two transects were laid out diagonally across each plot, each transect was 300 m long. For each transect, 100 points were recorded, resulting in 200 recordings per plot in total. Along each transect, every 3 m a pointer was placed on the ground and the nearest (distance not exceeding 15 cm) grass and forb species was recorded as well as the distance from the pointer to the grass or forb species. The herbaceous basal cover (%) was calculated following methods by Cottam and Curtis (1956).

Woody species composition and structure (measured as tree height and density)

The woody species composition and structure of each plot was determined in December 2009. Four belt transects of 100 m long and 4 m wide were laid out evenly across the plots. Tree heights and identities within each of the transects were recorded. Tree density was calculated for each plot by dividing the total number of trees found per plot by the area of the plot.

Statistical analysis

An analysis of variance (ANOVA) followed by Least Significant Difference (LSD) post-hoc tests was used to test for the effects of the burning treatments on soil nutrient levels. A repeated measures analysis of variance (RMANOVA) was used to analyse herbaceous plant biomass and grass quality (digestibility and grass leaf C:N ratio) in the different burning treatments, over the different months from January to June 2010. Ordination by Correspondence Analysis (CA) was carried out to separately analyse the grass (Table 2 in Appendix B), forb (Table 3 in Appendix B) and tree (Table 4 in Appendix B) species composition data. The Shannon diversity index was computed for plant species diversity (grass, forbs and trees separately). The effects of burning treatments on grass and forb basal cover (herbaceous vegetation structure) and tree density and height (woody vegetation structure) were analysed using ANOVA. ANOVA and RMANOVA were conducted using GenStat 11th edition. Ordination by Correspondence Analysis (CA) and Shannon Diversity Index were computed using CANOCO (version 4.56).

Results

Soil nutrients

Soil nutrients that were significantly affected by the burning treatments were N ($F_{(3.54)} = 13.64$, $n = 15$, $p < 0.001$), organic C ($F_{(3.54)} = 6.43$, $n = 15$, $p < 0.001$), K ($F_{(3.54)} = 6.34$, $n = 15$, $p < 0.001$), and P ($F_{(3.54)} = 4.20$, $n = 15$, $p = 0.01$). Mg ($F_{(3.54)} = 1.72$, $n = 15$, $p = 0.174$) and Ca ($F_{(3.54)} = 0.35$, $n = 15$, $p = 0.792$) were not significantly affected by burning treatments (Fig 2.1). N, P, C and K concentrations were highest in the absence of fire. In contrast, concentrations of these nutrients were lowest in the annually burned plots (Fig 2.1a, b, c & d respectively).

Plant biomass (herbaceous)

Herbaceous plant biomass was significantly affected by the burning treatments ($F_{(3.6)} = 17.52$, $p = 0.002$) (Fig 2.2). The control plot had a significantly higher plant biomass than the new plot, triennial burn plot and annual burn plot (Fig 2.2). Note that there was an accumulation of material in the unburned control plots, while the other plots were all burned at the beginning of the growing season. There were no significant differences in herbaceous plant biomass between any of the other burning treatments. Time (different months) had a significant effect on plant biomass, with Dec 09 – Mar 10 showing significantly lower plant biomass than the period Apr 10 – Jun 10 for all burning treatments ($F_{(6.48)} = 44.46$, $p < 0.001$) (Fig 2.3).

Plant quality (grasses)

The mean digestibility (%) of the dominant grasses was not significantly affected by the burning treatments (F $_{(3.6)}$ = 0.68, p = 0.594). Time (different months) had a significant effect on digestibility, with the highest values recorded in January 2010, declining steadily until June 2010 (F $_{(5.40)}$ = 82.83, p < 0.001) (Fig 2.4). The mean grass tissue C:N of the dominant grasses was not significantly affected by the burning treatments ($F_{(3,6)}$ = 1.58, P = 0.290). Time (different months) had a significant effect on grass tissue C:N ($F_{(5,40)}$ = 130.27, P < 0.001), with the highest values in January until March 2010, declining from April and lowest in May and June 2010 (Fig 2.5).

Herbaceous species composition and basal cover

There were no clear patterns on the ordination plots of the herbaceous species composition based on fire frequency. There was also no significant difference in the Shannon diversity index of grasses and forbs at the various burning treatments for grasses (F $_{(3.6)}$ = 2.23, p = 0.185) (Table 5 in Appendix B) and for forbs (F $_{(3.6)}$ = 1.24, p = 0.376) (Table 6 in Appendix B)). Grass basal cover was significantly affected by fire frequency (F $_{(3.6)}$ =7.96, p= 0.016). It was highest in the control plot followed by the new plot and the triennial burning treatments and lowest in the annual burning treatment (Fig. 2.6). Forb basal cover was similar among various burning treatments (F $_{(3.6)}$ =0.49, p = 0.701) (Fig. 2.7).

Woody species composition and structure

Clear patterns were found for the tree species composition in the various burning treatments. In the control plots, *Commiphora schimperi* and *Ziziphus mucronata* were common. In the new plots *Boscia foetida* and *Gymnosporia senegalensis* were common. In the triennial and annual burning treatment plots, *Acacia borleae* and *Ormocarpum trichocarpum* were common. Although different tree species were found in different burning treatments, fire frequency had no significant effect on the Shannon diversity index of tree species ($F_{(3.6)} = 3.91$, $p = 0.073$) (Table 7 in Appendix B).

We found significant effects of fire frequency on tree density ($F_{(3.6)} = 9.04$, $p = 0.012$) and tree height ($F_{(3.6)} = 5.60$, $p = 0.036$). Tree density was significantly higher in the control, new plot and triennial burning treatments than in the annual burning treatment (Fig. 2.8). Trees were taller in the control plot than in the new plot, triennial and annual burning treatments (Fig. 2.9).

Discussion

Soil nutrients

The soil nutrients tested were N, organic C, K, P, Mg and Ca. Although these soil nutrients are important for plant growth and development (Pietikainen and Fritze, 1995), nitrogen is usually the only nutrient which significantly increases herbage quantity (Risser and Parton, 1982). The concentration of N was lowest in the triennial plot. In contrast, other studies reported soil N to be lowest in plots subjected to more frequent fires due to volatilization (Briggs and Knapp, 1995; Fu et al., 2010). In our study the higher concentration of soil N in the annual plot than in the triennial plot may have been due to the presence of herbivores. Studies have shown that herbivores are found more frequently on annual burn sites because of low predation risk and high forage quality (Mills and Fey, 2005). Herbivore urine/fecal inputs are known to have appreciable levels of nitrogen (Cech et al., 2008). Therefore the presence of herbivores in the annual plot may have compensated for the losses of soil N via fire.

Soil organic C has a major influence on the physical structure of the soil, the soil’s ability to store water and the soil’s ability to form complexes with metal ions and supply nutrients (Dai et al. 2006). Loss of soil organic C can therefore lead to a reduction in soil fertility (Fu et al., 2010). In the present study soil organic C decreased with increasing fire frequency. In contrast to what we found, Dai et al. (2006) found that soil organic C was higher in annually burned plots than in unburned plots, due to increased rates of above- and belowground primary production in annually burnt plots. Scholes and Walker (1993) suggested that whether or not soil organic C increased or decreased under contrasting fire frequencies was dependent on fire intensity and changes in primary production resulting from the effects of fire. The effects of fire intensity on soil organic C is not well understood, more studies are needed to increase our understanding.

In the present study soil P generally increased with increasing fire frequency. This may be because in the burned plots P gets released from standing aboveground tissue (Mills and Fey, 2005). Soil K was higher in the unburned treatment than in the burned treatments whereas Mg and Ca were not affected by fire frequency. A study by Scholes and Walker (1993) suggests that soil cations such as Ca and Mg are rarely affected by fire frequency. The concentration of K, Mg and Ca ions in the soil can increase, decrease or be unaffected by fire (Cass et al., 1984; Scholes and Walker, 1993; Shackleton and Scholes, 2000; Mills and Fey, 2005; Dai et al., 2006). This is because the relationship between fire and soil nutrients is complex due to the interactions of many factors. Fire intensity is usually the most critical factor driving post-fire nutrient dynamics. To better understand the effect of fire on soil nutrients, more studies that take fire intensity into account are still needed.

Plant biomass and quality

Herbaceous standing plant biomass was significantly affected by fire frequency over time. The control plots had a higher biomass than any other burning treatment, which is not surprising since they had not been burned. Fire frequency did not have any significant effect on herbaceous plant biomass for any of the other treatment plots, the annual burned plots had higher plant biomass than the triennial and the new plots. Plant biomass was lowest in December 2009 in all plots, gradually increased over the course of the growing season until it declined during the dry season. The trend observed here may have been due to seasonal rainfall differences. For the year of the study, rainfall started late in December and increased until March and from May to June it declined. A number of studies have shown that plant biomass is low after a burn and then gradually increases in response to rainfall (Gujera and Owen-Smith, 2002; Fuhlendorf and Engle, 2004).

Plant quality was measured as digestibility and C:N ratio for the dominant grass species. The present study showed that fire frequency did not affect tissue digestibility and C:N ratios. This contradicts other studies that have shown that fire frequency influences herbaceous plant quality to varying degrees (Bigalke and Willan, 1984; Frost and Robertson, 1987; Andersen et al., 2005). The differences between these studies and the present study may be due to other factors such as the different soil types, e.g. the present study was carried out on the nutrient rich soils, basalt. Anderson et al. (2005)'s study was carried out on the nutrient poor soils, granite. As a result, the effect of fire frequency on forage quality may have been negligible on the present study because the forage was already high in nutrients due to the soils as opposed to the Andersen et al. (2005)'s study. Plants re-growing after a fire often have low cellulose and thus are easily digestible, and the concentrations of nitrogen and minerals is higher compared to unburned plants (Frost and Robertson, 1987; Johnson and Matchett, 2001). However, this increase in plant quality is transitory, lasting only for a few weeks at the beginning of the growing season (Van de Vijver et al., 1999). Thus apart from fire frequency, another important factor that influences herbage quality is leaf age or time since fire (Meissner et al., 1999; Rahim et al., 2008). The present study showed that digestibility and C:N ratio decreased with increasing maturity of the plants over time which concurs with the findings of several studies (Van Soest, 1965; Skerman and Riveros, 1990; Rahim et al., 2008).

Herbaceous species composition and structure

The present study found no response of the herbaceous species composition and diversity to fire frequency. This contradicts other studies that have shown that frequent fires changes the herbaceous species composition and increases diversity, while fire exclusion leads to a loss of many species (Uys et al., 2004; Oluwole et al., 2008). However, these studies were conducted in mesic savannas where herbaceous species respond significantly to fire frequencies (Uys et al., 2004). Our study was conducted in a semi-arid savanna where the effects of fire-herbivore interaction on herbaceous species is more important than fire alone (Smith et al., Submitted).

Forb basal cover was not affected by fire frequency whereas grass basal cover was strongly affected. Grass basal cover decreased with increasing fire frequency. This may be attributed to higher numbers of grazing herbivores as they prefer frequently burned plots. As a result, the high grazing pressure leads to lower grass basal cover. This finding concurred with several studies that have shown that frequent burning resulted in low basal cover while less frequent burning resulted in increased basal cover of grasses particularly in arid and semi-arid regions (Kennan, 1971; Robinson et al., 1979; Uys et al., 2004).

Woody species composition and structure

Our findings showed that fire frequency did not have a significant effect on woody species composition. However, the woody size structure and density decreased with increasing fire frequencies. Trees also were taller in the control plot than in any other burning treatments. This might be because frequent burning reduces tree height and keeps individual trees small (Higgins et al., 2007). The present study also found that tree density decreased with increasing fire frequency. These findings are similar to other studies (Hoffmann, 1999; Shackleton and Scholes, 2000) that have shown that high fire frequencies reduced woody species densities. However, some studies contradict the findings of this study. For example, Strang (1974) concluded that woody density was not affected by regular fires after comparing two paired sites (fire break versus an unburned area). In the fire trials in the KNP, Higgins et al. (2007) also found similar results to the present study, that fire frequency does not influence tree density but influences the size structure. The differences in these findings may be due to the effect of climate, an aspect that was not covered in this study (Bond et al., 2002).

Conclusion

Fire frequency had variable effects on all soil nutrients tested. Soil nutrients have been shown to be influenced by a number of factors (Shackleton and Scholes, 2000), the present study showed that in order to better understand the effects of fire frequency on soil nutrients future studies should take into account the effect of fire intensity as well and the presence of herbivores. Increasing fire frequency resulted in both decreasing tree height and tree density. Forb basal cover was not affected by fire frequency whereas grass basal cover strongly decreased with increasing fire frequencies. This result indicates that more grazing herbivores may have selected sites with high fire frequencies because of improved visibility and because of that the grazing pressure was higher on sites with high fire frequencies. As a result the grass basal cover was lower on sites with high fire frequencies. Species diversity of trees, forbs and grasses were not significantly affected by fire frequency. These findings are in line with other studies that have shown that fire frequency does not affect diversity of tree species (Van Wilgen et al., 2003; Higgins et al., 2007). Plant biomass was significantly affected by fire frequency, the control plot had higher biomass than the other burning treatments, although there were no differences between the burning treatments. Forage quality was not significantly affected by fire frequency. Therefore, the effect of fire frequency is more pronounced on the structure of vegetation rather than the composition, with more frequent fires reducing the structure of vegetation thus creating open savannas. As a result fire frequency can be used as tool to create open or closed savannas. Therefore fire frequency may drive herbivore selection through it effect on the vegetation structure. For all the characteristics tested (i.e. soil nutrients, vegetation structure and composition) the new plot showed similar results to the triennial burn on the EBPs. Thus, although the EBPs are at a relatively small scale they do appear to reflect the effects of fire regimes on the greater areas of the Kruger National Park in terms of soil nutrient status, herbaceous vegetation quality, and vegetation composition and density.

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Chapter 3: Effect of fire frequency on large mammalian herbivore distribution and behaviour in a South African semi-arid savanna

Abstract

This study investigated the effects of fire frequency on herbivore distribution, as well as the mechanisms underlying the distribution and seasonal herbivore behaviour in selected Experimental Burn Plots (EBPs) in the central region of the Kruger National Park, South Africa. The driving mechanisms investigated were soil nutrients, plant community structure and composition, seasonal forage quality and quantity, and potential predation risk. The study was conducted on the annual, triennial, and control (unburned) burning treatment plots (EBPs burned in the dry season, August) at Satara, N'wanetsi and Marheya sites, as well asplots (hereafter referred to as "new plots") located in areas adjacent to the EBPs at each study site. The new plots, which were burned at ~ 4 year return interval, were established to evaluate the effects of fire on animal distribution on small plots in relation to the surrounding area. Herbivore distributions and behaviour were monitored weekly. The distribution of all herbivore species combined was not affected by fire frequency. When herbivores were grouped into their feeding guilds and the effect of fire frequency assessed over the wet and dry season, only mixed-feeders (e.g. impala) were found to be significantly affected by fire frequency. Mixed feeders were found in higher abundance over time on the control and annually burned plots than the triennially burned and new plots, whereas grazers were observed in greater abundance in the dry season than the wet season irrespective of the burning treatment. None of the mechanisms tested was correlated to herbivore distribution. Additionally, the behaviour of all herbivore species was predominantly influenced by seasonally-induced changes to their environment rather than fire

frequency. In conclusion, it appears that fire frequency was not the main driver affecting herbivore distribution and abundance. Additional studies are needed to further investigate the effects of fire frequency and season on herbivore distribution and abundance patterns.

Introduction

Herbivore behavior, abundance and distribution patterns, or choice of habitat, are affected by a number of factors such as the availability of resources (forage quality and quantity) and predation risk (Mapiye et al., 2008). Disturbances such as fire play a major role by influencing the forage quality and quantity available to herbivores while changing their exposure to predators (Mills and Fey, 2005; Mapiye et al., 2008; Burkepile et al., In prep). Fire can cause changes in soil nutrients, forage quality and quantity, and vegetation composition and structure which in turn may impact herbivore distributions (Bergstrom and Skarpe, 1999). Plants respond to the increased soil nutrients, higher light availability and altered plant species composition following a burn by increasing biomass production (Mills and Fey, 2005). Shortly after a burn, forage quality is generally high and quantity is low (Rowe-Rowe 1982). As the growing season progresses, forage quality declines and quantity increases (Fryxell, 1990). Herbivores, particularly grazing herbivores, are attracted to the recently burned areas due to the flush of green growth and higher quality forage following a fire (Van de Vijver et al., 1999). The effects of fire frequency on soil nutrients, forage quality and quantity and how it may drive herbivore distributions and abundance are not well known (Mapiye et al., 2008).

Tree and shrub cover declines significantly with increasing fire frequency (Trollope, 1982; Shackleton and Scholes, 2000). As vegetation cover decreases with increasing fire frequency, visibility increases (and thus the ability to detect predators). Many herbivores prefer areas that have been frequently burned (Bigalke and Willan, 1984; Mapiye et al., 2008), while others disperse randomly irrespective of the region's fire history, or prefer areas that are not frequently burned (Van Langevelde et al., 2003). In addition, season may be a factor influencing herbivore distributions in areas with different fire frequencies. For instance, in the wet season, grazers prefer frequently burned areas because of high forage quality (Fryxell, 1990; Wronski, 2003). Visibility is also low, and thus herbivores spend more time being vigilant due to higher predation risk (Funston et al., 1994). In the dry season, however, frequently burned areas do usually not have much forage remaining, thus grazers tend to forage on the infrequently burned areas (Wronski, 2003). Moreover, visibility is high even in the infrequently burned areas, and thus the predation risk is generally decreased (Bergstrom and Skarpe, 1999).

The aim of this study was to determine the effect of fire frequency on large mammalian (greater than 5 kg) herbivore distribution and behaviour, as well as the potential mechanisms driving their movement. To accomplish these objectives, herbivore abundance and behaviour was monitored in the annual, triennial, and control (unburned) burning treatments plots (EBPs burned in the dry season) at Satara, N'wanetsi and Marheya sites in the Kruger National Park, South Africa. Additional plots (hereafter referred to as the "new plots") were established in the landscape adjacent to the treatment plots at each site to assess…The driving mechanisms investigated were soil nutrients (nitrogen, organic carbon, potassium, phosphorus, magnesium and calcium), plant community structure and composition (tree density, tree height, grass cover, forb cover, and species diversity of trees, grasses and forbs), and forage quantity (herbaceous biomass) and forage quality (grass nutrient content).

The key research questions addressed were:

1. What is the effect of fire frequency on the abundance of all herbivore species combined?

2. Do soil nutrients and plant community structure and composition influence herbivore distribution and abundance among areas burned at different frequencies?

3. Does the abundance of the different herbivore feeding guilds (mixed-feeders, grazers and browsers) differ in the various fire treatments during the dry and wet season?

4. Does the forage quality and quantity influence the abundance of grazing (grazers) herbivores in sites burned at the different fire frequencies during the wet vs. dry season?

5. What is the behaviour of herbivores present in sites burned at different frequencies during the wet and dry season, that is, what activities do herbivores engage in (e.g., feeding, moving, standing) and which of those activities take up most of their time between the wet and dry seasons?

6. What is the effect of fire frequency on the predation risk in the wet and dry season and does it affect herbivore seasonal abundance and behaviour?

Methods and materials

The study was carried out from July 2009 to June 2010 in the Experimental Burn Plots (EBPs) of the Kruger National Park, South Africa. EBPs included in this study consisted of the annual- and triennial-fire interval as well as the control plots (unburned) at the Satara, N'wanetsi and

Marheya sites. In addition, plots (hereafter referred to as "new plots") were established in the landscape adjacent to the EBPs at each study site. These areas experienced a mean fire return interval of every four years at each study site. These new plots were established to evaluate the effects of fire on animal distribution on small plots in relation to the surrounding area. This resulted in a total of 12 plots (3 study sites x 4 fire treatments).

Herbivore day surveys

Herbivore surveys were conducted on the selected EBPs during the day following methods used by Burkepile et al. (in prep). Surveys were evenly distributed over three-hour time periods (6h00-9h00, 9h00-12h00, 12h00-15h00, 15h00-18h00), roughly covering 12 hours of daylight. Each observation began with a 3-5 minute acclimation period. The abundance of all mammalian herbivores (>5kg) (Skinner and Chimimba, 2005) was recorded twice weekly from July 2009 - June 2010. This was done by driving in a vehicle along the perimeter of each plot at idle speed (approx. 10km.hr^{-1}). The number of individuals that were sighted per herbivore species was recorded as well as the gender and age of the animals (juvenile (J) or adult (A)). The precise location of the herbivore(s) was recorded by noting the compass bearing and the distance from the observation point (using a handheld GPS) with a laser rangefinder (Bushnell Yardage Pro 500DX).

Herbivore night surveys

Observations were conducted between 20h00 – 01h00 from (September 2009 – June 2010). Study plots were swept with a spotlight in search for the reflected eye shine of animals while driving a vehicle along the perimeter of each plot at idle speed (approx. 10km.hr^{-1}). When animals were spotted, the vehicle was stopped and the engine switched off. Binoculars and spotlights were used to record the species, number of individuals per species, activity and gender (if possible). Each observation would start after three to five minutes acclimation time to avoid behaviour disturbance by the spotlight/observer's presence. At least two EBP sites were surveyed per night (either Satara and N'wanetsi or Satara and Marheya, or Marheya and N'wanetsi). Surveys were conducted on two nights per week, resulting in three surveys per EBP site every two weeks.

Herbivore dung surveys

The numbers of the various mammalian herbivore species (> 5kg) were indirectly recorded by conducting dung sample surveys on the selected EBPs. These surveys were done once a month from July 2009 - June 2010. Seven transects (40m x 2m) were established in all study plots and the individual dung piles of the various herbivore species were identified and recorded. The age of the dung piles was also determined and categorised (new = fresh soft dung and old = hard dung). Recorded dung piles were removed from all transects to ensure they were only counted once.

Herbivore behaviour (time allocation of activities)

Behavioural observations were conducted during the daytime herbivore surveys (06h00 – 18h00) from July 2009 to June 2010. The months July 2009 – September 2009 and April 2010 – June 2010 represented the dry season and October 2009 – March 2010 represented the wet season. One individual per herbivore species present was selected as a focal animal. Each observation began after a 3-5 minute acclimation period. The behaviour (Appendix C) was recorded instantaneously at 15-second intervals for 15 minutes, resulting in 60 recordings per individual observation. A stopwatch with a timer was used to mark 15-second intervals. To avoid potential issues of non-independence, behavioural observations were not conducted on more than one individual of the same herd on a given day. Care was taken to record equal numbers of males and females. Juvenile individuals were excluded from the observations. The presence of any other species nearby was also recorded. Prior to the onset of every observation the species, gender (if known) and age (Juvenile/Adult) of the individual was recorded. The plot in which the animal was found, the number of other individuals in the herd (if any), and the presence of any other species nearby was also recorded.

Visibility measurements

Visibility measurements were conducted to determine predation risk for the herbivores. Measurements were taken on a monthly basis from January 2010 – June 2010. Visibility measurements only started in January 2010 because prior to January there was no adequate plant growth. All the plots had been burned in the dry season, except for the control plots. Rainfall started during late October 2009 and adequate plant growth for visibility measurements was only present from January 2010. Data collection took place between 10h00 and 15h00 to avoid visibility differences due to changed daylight conditions. A 1.2 x 0.6 m brown cardboard, cut roughly in the shape of a lion, was used as a predator imitation. To measure the visibility of the prey species for its predator, one person holding the cardboard was stationary in the centre of the study plot. Then a second person measured the distance to the stationary person once the visibility of the cardboard had dropped to approximately 50% using a 50-m measure tape. Visibility measurements were done at two heights, 0.8 m and 1.5 m. The lower height of 0.8 m is roughly the height of the eyes of a warthog and impala, whereas 1.5 m is roughly the height of the eyes of white rhino, buffalo, zebra and wildebeest. Measurements were taken at five random locations for all 4 cardinal points (North, South, East and West) in each study plot, resulting in

240 measurements in total per month (5 locations per plot x 4 cardinal points per location x 12 plots).

Soil nutrients

In September 2009, five soil samples were collected per plot (after the fires but before the onset of the rains). Soil samples were collected once based on the assumption that soil chemistry does not vary appreciably over time (Fynn et al., 2003). Samples were collected at about 20 m intervals across the centre of the plot at a depth of 10 cm using a soil auger. As a result, 60 samples were collected (5 samples x 4 fire treatments x 3 study sites). Samples were analysed for total nitrogen, organic carbon, phosphorus, potassium, magnesium, and calcium, at the Soil Science laboratory of the University of KwaZulu-Natal, South Africa.

Herbaceous plant biomass

Herbaceous plant biomass production was measured using a standard disc pasture meter (1.5 kg metal disc, 45 cm in diameter) (Bransby and Tainton, 1977; Zambatis et al., 2006). At each plot, 200 measurements per month were randomly taken (December 2009 – June 2010) spread evenly throughout the plot. From August – November 2009, measurements were not taken because the plots had been burned (except for the control) and due to the lack of rain not enough plant growth took place until December therefore herbaceous biomass was negligible in August until November 2009. Measurements were taken within plots at locations at least 3 m apart to ensure independence of individual measurements. Additionally, different starting points for the measurements were selected for each survey, to ensure data independence over time. Existing calibration equations developed by Zambatis et al. (2006) for the Kruger National Park were used to convert disc pasture readings to estimates of standing biomass.

Plant quality

Herbivore forage quality of the dominant grass species (Appendix A) was determined in each study plot using two methods: digestibility as cellulase dry matter disappearance (CDMD) and leaf C:N ratio. For the CDMD analysis, 10 g of plant material of each grass species was collected by clipping their tufts to ground level. For the C:N ratio analysis, 20 leaves per grass species were collected from each plot. Samples were collected on a monthly basis from December 2009 to June 2010. All samples of both leaves and tufts were oven-dried at 60 ˚C for 48 hours and later milled, with 5 g and 2 g subsamples used for CDMD and C:N ratio analysis, respectively**.** The CDMD analysis was carried out at the Grassland Science laboratory of the University of KwaZulu-Natal. The C:N ratio analysis was carried out at the Chemistry laboratory of the University of KwaZulu-Natal.

Herbaceous species composition and structure

Herbaceous (forb and grass) species composition data were collected in March 2010. The point-to-tuft-distance method was used to record the species composition in each plot (Cottam and Curtis, 1956; Hardy and Tainton, 1993). Two transects were laid out diagonally across each plot. For each transect, 100 points were recorded, resulting in 200 points per plot in total. Along each transect, every 3 m a pointer was placed on the ground and the nearest (distance not exceeding 15 cm) grass and forb species was recorded as well as the distance from the pointer to the grass or forb species. The herbaceous basal cover (%) was calculated following methods by Cottam and Curtis (1956).

Woody species composition and structure (measured as tree height and density)

The woody species composition and structure of each plot was measured in December 2009. For that, four belt transects of 100 m long and 4 m wide were laid out evenly across the plots. All individual trees were located within the transects and their height recorded. Tree density was calculated for each plot.

Statistical analysis

An Analysis of Variance (ANOVA) was used to test for the effects of burning treatments on the herbivore densities during the day and night and to also determine if there were any differences between the day and night surveys. The density for all herbivore species combined were calculated (per ha) for the day and night distribution at the different burning treatments. Densities were standardized based on the number of surveys conducted.

A repeated measures of analysis of variance (RMANOVA) was used to test the effect of burning treatments and season on the distribution of herbivores grouped into their feeding guilds. The effect of burning treatment and season on visibility (measure of predation risk) was also tested using RMANOVA.

Two-tailed Pearson correlation tests ($\alpha = 0.05$) were conducted to assess the relationship between soil nutrients, vegetation-based (plant community structure, herbaceous biomass and grass nutrient content) and herbivore-based (herbivore density and dung count) variables. For each correlation analysis, there was a total of twelve points, one representing each of the four burning treatment plots on each of the three study sites. This analysis was used to identify those variables mostly strongly contributing to variation in herbivore density and dung counts across plots. Analyses were performed for 1) all species combined, and 2) for grazing herbivores only (Table 3.1). Note that only the grazing herbivores were subjected to correlation analysis with herbaceous biomass and grass nutrient content (forage quality and quantity) because they are the ones that feed on grass whereas the browsers predominantly feed on woody plants and shrubs.

Also only the dung count data were used to investigate seasonal distributions. This was because the dung count data integrates herbivore distribution over a longer time period whereas the survey data indicates distribution at a particular time. In the wet season, some surveys were missed because the terrain was inaccessible to vehicles. Also note that herbivore survey data were also analysed to species level and the findings were not significantly different, as a result for the densities we only presented results for all herbivore species combined. All the statistical analyses were conducted using GenStat 11th edition. For all analyses, significance was set at $P \leq 0.05$.

Results

Herbivore day and night distribution

A total of 1959 individual mammalian herbivores (> 5kg) representing 12 herbivore species (Table 3.1) were recorded during 145 day and 81 night surveys. The dominant herbivore species recorded were Burchell's zebra (*Equus burchelli*; 27%), impala (*Aepyceros melampus*; 27%) and Cape buffalo (*Syncerus caffer*; 26%). Burchell's zebra and Cape buffalo are grazers whereas impala are mixed-feeders (Table 3.1).

The density of all herbivore species combined was not affected by burning treatment ($F_{(3.6)} = 0.74$, $p = 0.564$). Herbivore densities during the day were not significantly different from densities at night ($F_{(3.6)} = 0.80$, $p = 0.537$).

We found no correlation between the distribution of all herbivores combined (density) and soil nutrients and vegetation composition and structure, for all of the coefficients $p > 0.05$. None of the soil nutrients and vegetation variables appeared to contribute to the variation in herbivore distribution across all plots (Table 3.2).

Herbivore seasonal distribution

For the herbivore dung surveys, herbivores were grouped into their feeding guilds i.e. mixed-feeders, grazers and browsers. Mixed-feeders were significantly affected by the burning treatments ($F_{(3.6)}$ = 8.31, p = 0.015) (Fig 3.1a). The number of dung piles was significantly higher for the control and 1yr than in the new plot and 3yr (Fig 3.1a). Season did not affect mixed-feeders ($F_{(1.8)}$ = 2.26, p = 0.172). Grazers were not affected by burning treatment ($F_{(3.6)}$ = 1.06, p = 0.433) (Fig 3.1b). Season affected grazers ($F_{(1.8)}$ = 6.56, p = 0.034), with more dung piles observed in the dry (4.83 ± 0.626) season than the wet (2.57 ± 0.626) season. Browsers were not affected by any of the burning treatments ($F_{(3.6)}$ = 0.56, p = 0.658) (Fig 3.1c) or season ($F_{(1.8)}$ = 1.34, p = 0.280).

There was no significant correlation between the seasonal distributions of grazers and forage quality and quantity. Forage quality and quantity variables appeared not to contribute to the grazers' seasonal distributions (Table 3.3).

Herbivore seasonal behaviour

The behaviour of all herbivores differed in the two seasons irrespective of the burning treatments. In the dry season, herbivores spent most of the time moving while in the wet season they predominantly fed. Also, in the wet season they were more vigilant whereas in the dry season they were not vigilant. To illustrate this, an example for the behaviour of impala in a triennial burning treatment has been included (Fig 3.2) (note that all herbivores showed similar trends in the two seasons).

Visibility (measure of predation risks)

Visibility at both eye heights was not affected by burning treatments, for the herbivores with short eye height ($F_{(3.6)} = 4.31$, $p = 0.061$) and for the herbivores with tall eye height ($F_{(3.6)} = 3.87$, $p = 0.075$). Season had a significant effect on the visibility of all herbivore species, for the herbivores with short eye height ($F_{(1.8)} = 9.17$, $p = 0.016$) and for the herbivores with tall eye height ($F_{(1.8)} = 24.40$, $p = 0.001$). The visibility for all herbivore species was significantly higher in the dry season than in the wet season (Fig. 3.3).

Discussion

Herbivore distribution

The present study showed that the distribution of all herbivores combined was not affected by fire frequency. This may imply that the regrowth and the forage quality on the control plots may have been quite high which would make them comparable to the burned plots. As a result herbivore utilisation on all plots may have been evenly spread. This contradicts the study conducted by Burkepile et al. (in prep) that showed that fire frequency affected herbivore abundance, with the greatest numbers in the most frequently burnt plots and the lowest numbers in the unburned areas. Burkepile et al. (in prep) study was conducted in the same plots as the current study. The differences in the findings between these two studies may be due to other factors such a rainfall, an aspect not addressed in either of the two studies. Rainfall plays an important role in herbivore distributions (O'Connor, 1994) and can vary from year to year.

The present study also showed that herbivore distribution was not correlated to the soil nutrients and plant community structure and composition across plots, contrary to what was predicted. Mills and Fey (2005) showed that herbivores were more concentrated on annual burn plots with higher soil micronutrients than the unburned plots in the southern region of KNP. The differences in the findings of the present study and Mills and Fey (2005) could be due to soils differences between the two study areas. Soils from the present study (in the central region of KNP) are clayey and derived from basalt parent material while those ones in Mills and Fey (2005) are sandy and derived from granite parent material. Basalt soils have an inherently higher nutrient status than granitic soils (Shackleton and Scholes, 2000). Burkepile et al. (in prep) found similar results to the present study, where herbivore distribution was not significantly correlated to plant community structure and composition across all plots.

Herbivore seasonal distributions

The current study showed that mixed-feeders were the only feeding guild affected by fire frequency. However, mixed-feeders were not affected by season. Higher numbers of dung piles were found in the control and the annual burned plot than in the new plot and the triennial plot. The annually burned plot might be favoured by mixed-feeders because it consists of green flush and the nutrient content of the grass is high (Bergstrom and Skarpe, 1999; Mills and Fey, 2005). The control plot may be favoured by mixed-feeders because of the abundant browse material, due to the lack of fire (Shackleton and Scholes, 2000; Sankaran et al., 2005; Higgins et al., 2007).

Grazers were not affected by fire frequency. However, although the difference was not statistically significant, the control plots tended to have the lowest number of grazers compared to the other plots. Grazers may favour the burned plots over unburned plots due to the palatable nutritious food that was readily available (Mills and Fey, 2005). Other studies also showed that grazers are more abundant in burned plots than unburned plots due to high forage quality in burned plots (Bigalke and Willan, 1984; Liedloff et al., 2001; Sensening et al., 2010). Grazers in the present study were significantly affected by season. In all burning treatments, more grazers were observed in the dry season than in the wet season. During the wet season, food resources are readily available and thus grazers disperse anywhere and do not spend long period of time in one area (McNaughton, 1990). In the dry season, food resources are limited and grazers search for areas that were not heavily utilized in the wet season and they spend longer periods of time in one area (McNaughton, 1990).

Browsers were not affected by fire frequency in the present study. These findings are supported by Burkepile et al. (in prep) who showed that the distribution of browsers was not influenced by the different burning treatments. It is difficult to explain these findings because of the limited studies on how fire frequency affects browser distributions (Mapiye et al., 2008). Season did also not affect browsers. Literature on seasonal effects on browser distribution is very limited (Bergstrom and Skarpe, 1999). Therefore, more studies on the effect of fire frequency and season on the distribution of browsers are needed.

The present study found no correlation between forage quality and quantity on grazers' seasonal distributions across all plots. Other studies (Funston et al., 1994; Bergstrom and Skarpe, 1999) show that fire frequency does affect grazing herbivore seasonal distributions due to forage quality and quantity. The frequently burned areas have a low biomass but high forage quality in the early wet season. In the dry season, forage quantity is higher and quality is lower.

Herbivore seasonal behaviour and predation risk

Herbivore behaviour was not affected by fire frequency. Season was the predominant driver of the behaviour and distribution of mammalian herbivores. In the wet season, herbivores spent most of the time feeding, whereas in the dry season they were mainly moving around. This might be due to the fact that in the wet season forage is abundant whereas in the dry season it is scarce (Bergstrom and Skarpe, 1999). Therefore, in the dry season herbivores may spend more time moving around in search of forage. In the wet season, herbivores were found being highly vigilant whereas in the dry season they were not. This might be because of the visibility being significantly lower in the wet season than in the dry season (Fig 3.3). As a result herbivores had to be more aware of predators in the wet season (Fryxell, 1990; Funston et al., 1994; Schmitz et al., 1997).

Conclusion

Overall this study showed that fire frequency alone may have not been the main driver influencing herbivore distributions. Instead other factors such as fire intensity (which was not investigated in this study) might be important. Other studies have shown that fire intensity influences herbivore distributions (Mills and Fey, 2005; Mapiye et al., 2008). More intense fires have been shown to improve visibility thus reducing predation risk (Govender et al., 2006). However, this aspect is not well understood and more studies to investigate the interaction between fire frequency and fire intensity on herbivore distributions are needed. The behaviour of all herbivore species were predominantly influenced by seasonal-induced changes to their environment rather than fire frequency. Therefore, fire frequency combined with season may be one of the main factors i herbivore distributions and behaviour. None of the mechanisms tested correlated with herbivore distributions. However, the possibility that these mechanisms are the driving factors of herbivore distributions or choice of habitat cannot be ruled out, because fire frequency has been shown to impact on herbivore distributions in other studies. Further studies to investigate the role these factors play in shaping herbivore distribution or habitat choice in semi-arid savannas are still needed. The EBPs do provide the platform for future studies as they have shown that they do reflect the surrounding areas. Herbivore distributions on the new plots were similar to the triennial burned plot on the EBPs.

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Chapter 4: Conclusion

The aim of the project was to determine the effect of fire frequency on herbivore distribution and behaviour. Firstly the project investigated the effect of fire frequency on the potential mechanisms driving herbivore distribution and behaviour. The mechanisms investigated were soil nutrients, herbaceous biomass and forage quantity and quality, vegetation structure and plant species composition. The results of the study have shown that fire frequency has variable effects on soil nutrients. Forage quantity significantly decreased with increased fire frequency. Fire frequency had no significant impact on forage quality, and the species diversity of trees, forbs and grasses. Grass basal cover was higher in infrequently burned areas whereas the basal cover of forbs was not altered by fire frequency. Areas with frequent fires had fewer and shorter trees than areas with infrequent fires. The first part of the project has shown that the effects of fire frequency are more pronounced on the vegetation structure, which influences predation risk for herbivores rather than resources.

The second part of the project investigated how the findings above may have altered herbivore distributions and behaviour. Findings from this study showed that none of the tested mechanisms appeared to alter herbivore distributions. This is similar to a study conducted by Burkepile et al. (in prep) which was done at the same sites. They also found no indication that herbivore distribution was correlated to the potential driving mechanisms. The distribution of all herbivore species combined was not affected by fire frequency. Thereafter the effects of fire frequency and season on the distribution of different feeding guilds of herbivores were investigated. Fire frequency did not have an impact on the distribution of grazers and browsers. Mixed-feeders were significantly higher in the control and annually burned plots than the new plot and triennially burned plot. Season did not have a significant impact on the distribution of browsers and mixed-feeders. Grazers were significantly affected by season, with more grazers seen on the plots in the dry season than the wet season. The behaviour and predation risk of all herbivore species were predominantly influenced by seasonal-induced changes to their environment rather than fire frequency.

The results of this study have shown that the effect of fire frequency was more pronounced on predation risk for herbivores. The main reason for herbivores selecting more frequently burned plots may be the improved visibility conditions and the availability of forage. A number of studies have shown that the presence of predators in a system can cause changes in the behaviour of prey (Ripple and Bescha, 2004). These behavioural changes reflect the need for herbivores to balance demands for food and safety, which is what was observed in the present study. Also, Schmitz et al. (1997) indicated that the effects of predators on behaviour of prey species may be more important than direct mortality. The present study may indicate that fire frequency can be used as a tool to indirectly influence herbivore distributions through vegetation changes.

It is possible that the effects of fire frequency were less pronounced with regard to forage quality as the study area was on nutrient rich basalt soils. As a result the forage may have been already high in nutrients. More studies are needed on nutrient poor soils (e.g. granite soils) to determine how fire frequency alters the quality of forage. Additionally, I found that herbivore response to fire frequency varied between the wet and dry season. However, the present study has shown that fire frequency is not the main factor influencing herbivore distributions. To have a more holistic understanding of what drives herbivore distributions, more studies examining the interaction between a number of factors (e.g. fire intensity, fire season and rainfall) are needed.

The EBPs in Kruger National Park provide a platform for such studies. Not only do they provide data on various fire regimes (fire season, intensity and frequency), they also include an environmental gradient (from high rainfall in the West to low rainfall in the East; and from nutrient-rich (basalt) soils in the North to nutrient-poor (granite) soils in the South.

As observed in the present study the EBPs do reflect what happens at landscape level, the new plots showed similar results to the triennially burned plot of the EBPs. Therefore the EBPs can provide useful information for management implications. They can provide a better understanding on how fire regimes can be used as a tool to drive herbivore distributions along the environmental gradient not only in the KNP but in other similar savanna systems as well.

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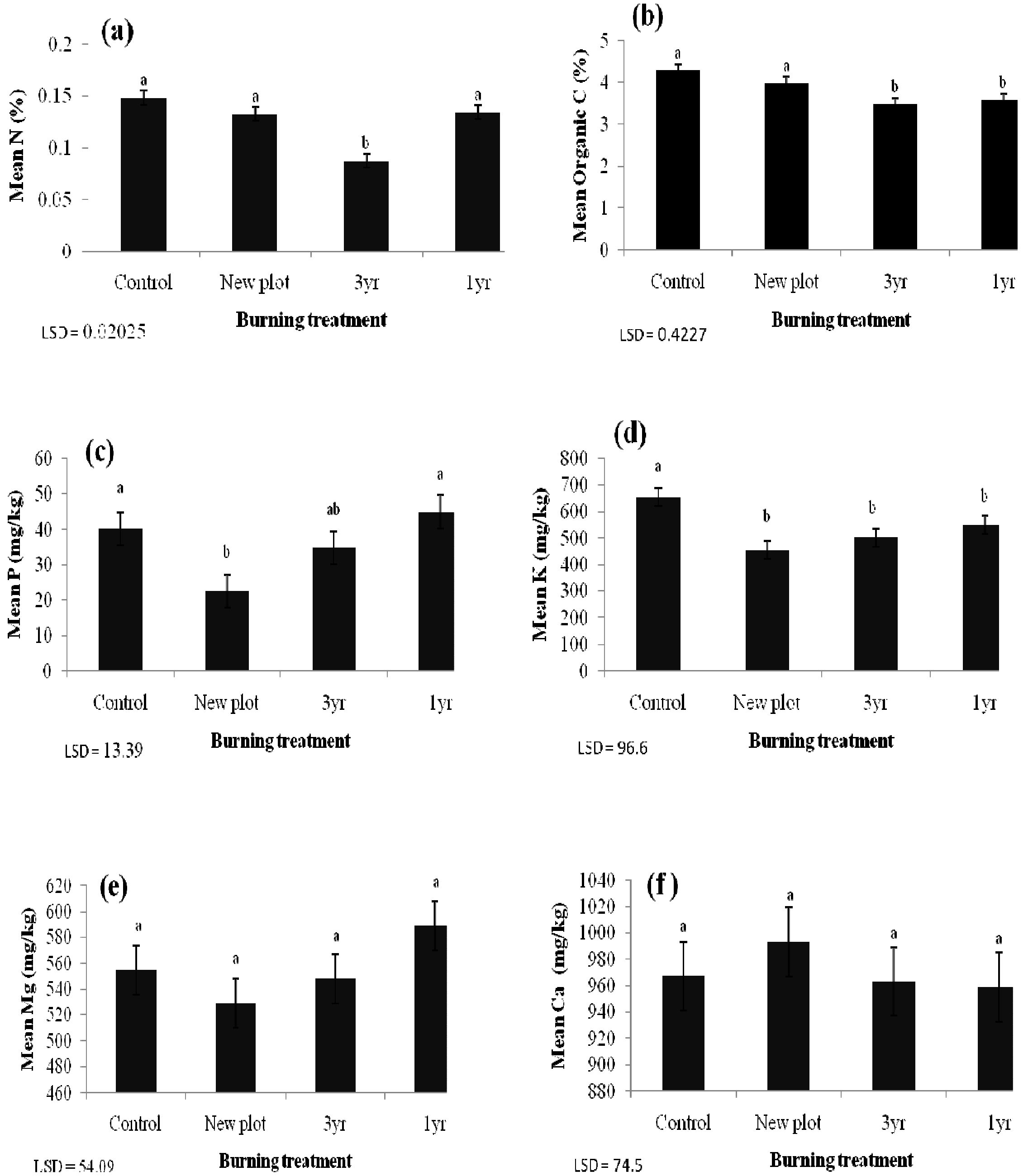

Figure 2.1 Mean soil nutrients content (±se) for the control (unburned), new plot, 3yr and 1yr EBPs at the Satara, N'wanetsi and Marheya, study sites, Kruger National Park, South Africa (n = 15 samples for each burning treatment). Different letters indicate significant differences ($P<0.05$). LSD = least significant difference of means at 5% level.

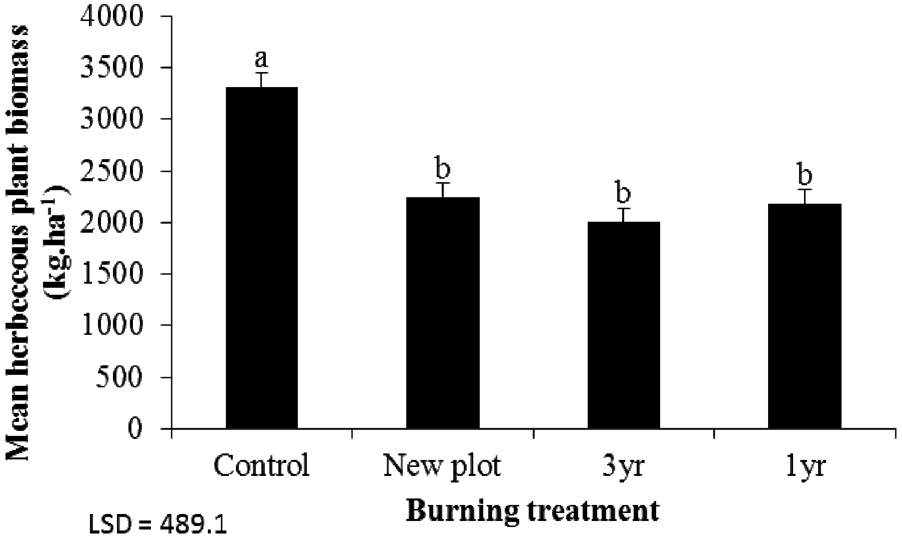

Figure 2.2 Mean herbaceous plant biomass (±se) for the control (unburned), new plot, 3yr and 1yr EBPs at the Satara, N'wanetsi and Marheya study sites, Kruger National Park, South Africa (n =15 samples for each burning treatment). Different letters indicate significant differences ($P<0.05$). LSD = least significant difference of means at 5% level.

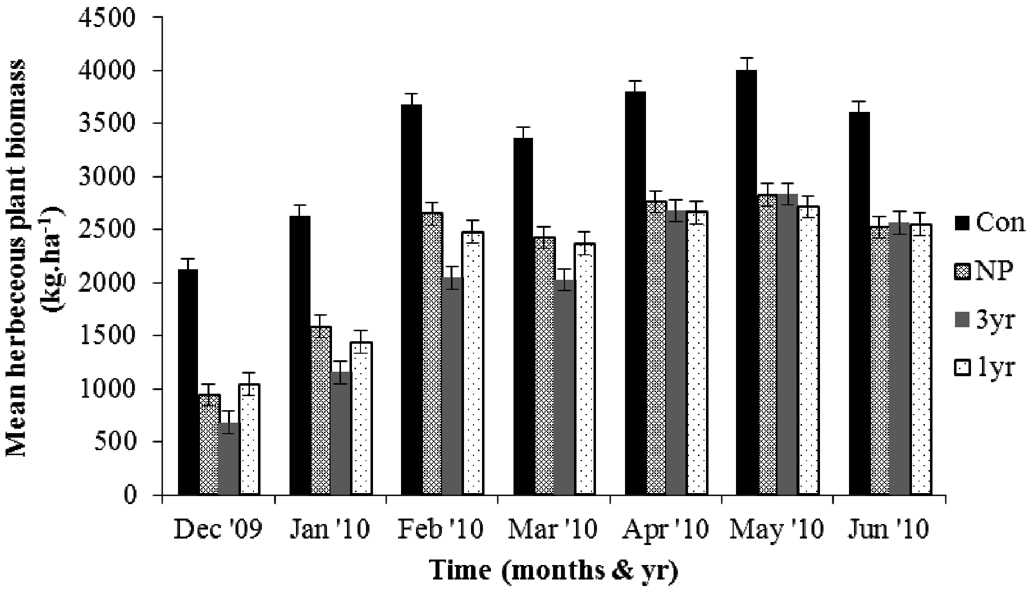

Figure 2.3 Mean herbaceous plant biomass (±se) from December 2009 until June 2010 for the control (unburned), new plot, 3yr and 1yr EBPs at the Satara, N'wanetsi and Marheya study sites, Kruger National Park, South Africa (n =15 samples for each burning treatment). Con = control and NP = new plot.

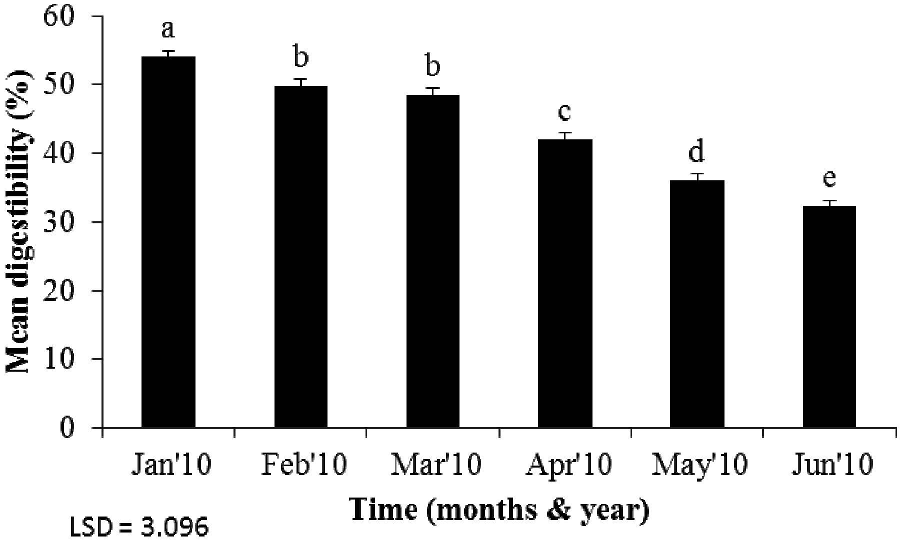

Figure 2.4 Mean digestibility (%) of the dominant grass species (± se) for the control (unburned), new plot, 3yr and 1yr in the EBPs at the Satara, N'wanetsi and Marheya study sites, Kruger National Park, South Africa from January 2010 to June 2010 (n = 44). Different letters indicate significant differences (P<0.05). LSD = least significant difference of means at 5% level.

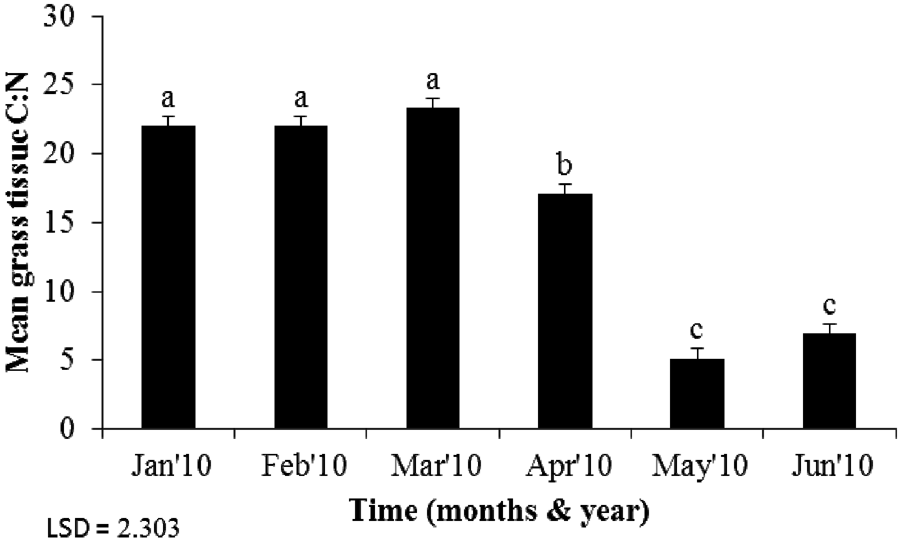

Figure 2.5 Mean grass tissue C:N of the dominant grass species (± se) for the control (unburned), new plot, 3yr and 1yr in the EBPs at the Satara, N'wanetsi and Marheya study sites, Kruger National Park, South Africa from January 2010 to June 2010 (n = 44). Different letters indicate significant differences (P<0.05). LSD = least significant difference of means at 5% level.

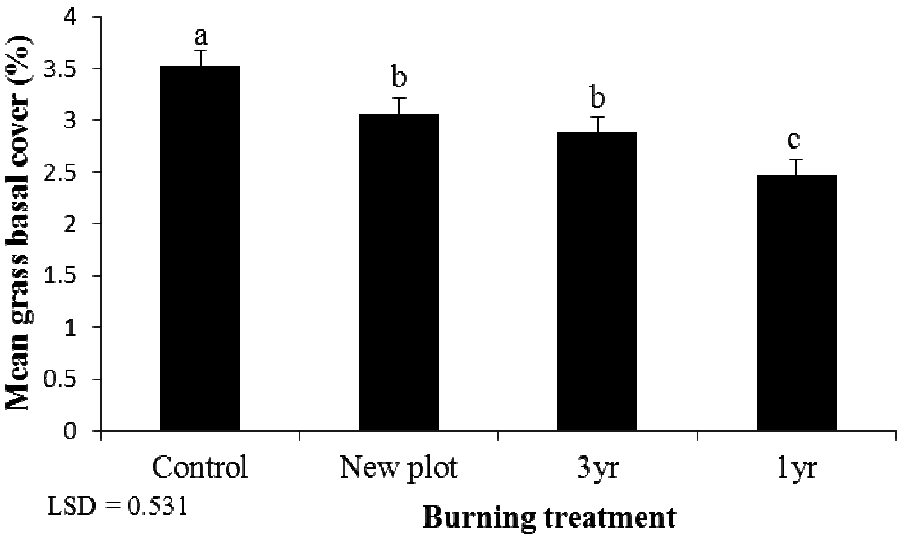

Figure 2.6 Mean grass basal cover (±se) for the control (unburned), new plot, 3yr and 1yr EBPs at the Satara, N'wanetsi and Marheya study sites, Kruger National Park, South Africa. Different letters indicate significant differences ($P<0.05$). LSD = least significant difference of means at 5% level.

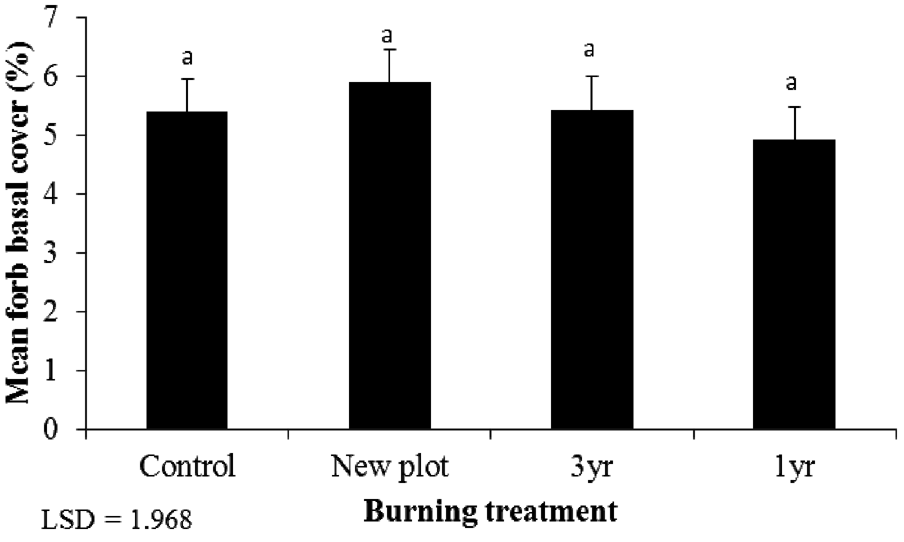

Figure 2.7 Mean forb basal cover (±se) for the control (unburned), new plot, 3yr and 1yr EBPs at the Satara, N'wanetsi and Marheya study sites, Kruger National Park, South Africa. Letter a above the bars indicate that there was no significant differences ($P>0.05$).

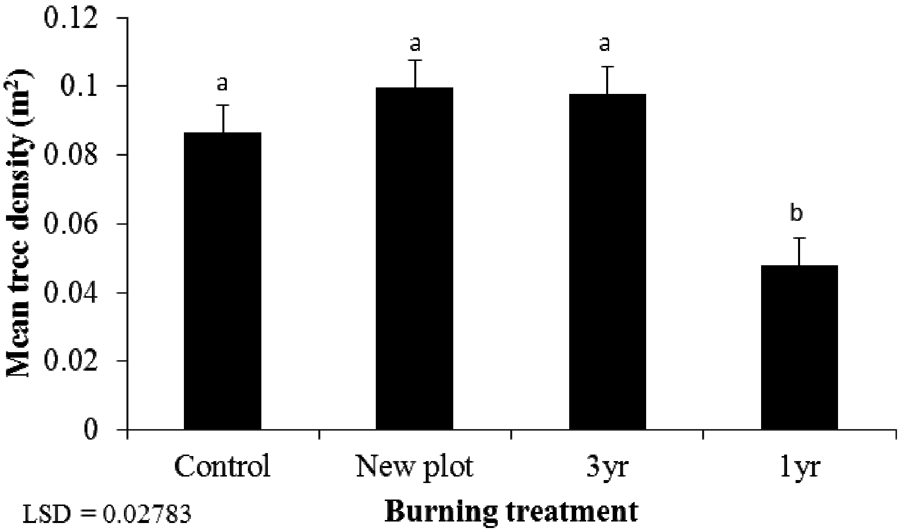

Figure 2.8 Mean tree density (±se) for the control (unburned), new plot, 3yr and 1yr EBPs at the Satara, N'wanetsi and Marheya study sites, Kruger National Park, South Africa. Different letters indicate significant differences (P<0.05). LSD = least significant difference of means at 5% level.

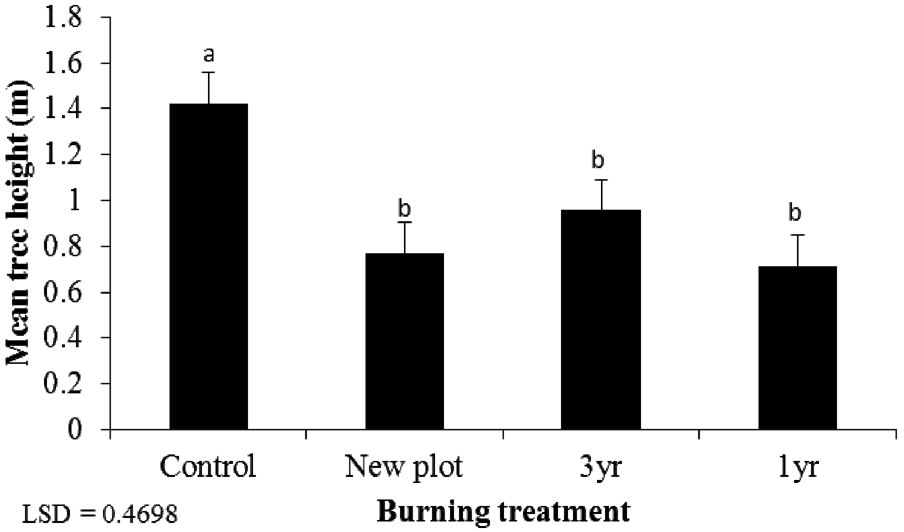

Figure 2.9 Mean tree height (±se) for the control (unburned), new plot, 3yr and 1yr EBPs at the Satara, N'wanetsi and Marheya study sites, Kruger National Park, South Africa. Different letters indicate significant differences (P<0.05). LSD = least significant difference of means at 5% level.

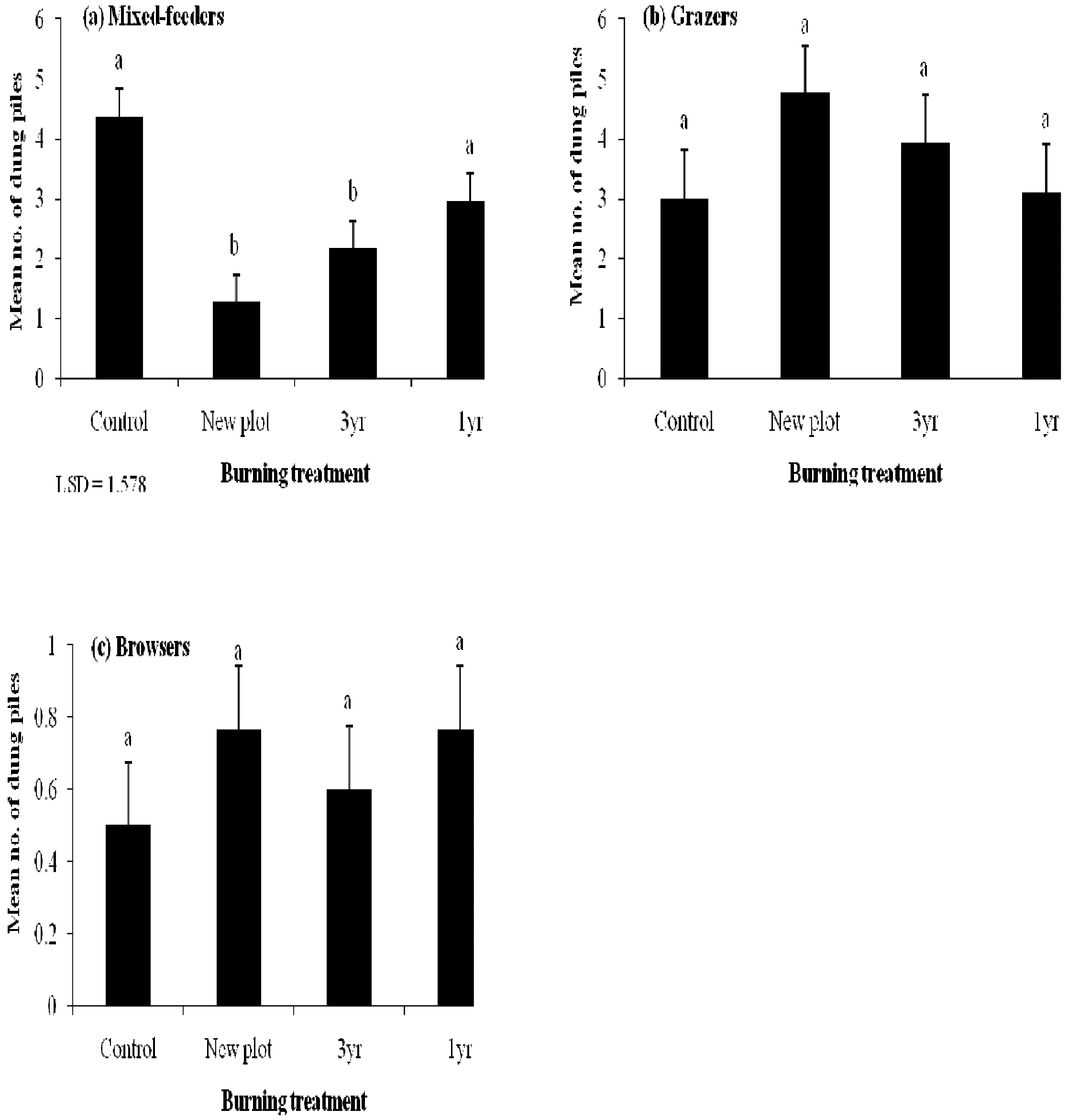

Figure 3.1 Mean (± se) number of dung piles per burning treatment for herbivores in their feeding guilds at the control, new plot, 3yr and 1yr EBPs at Satara, N'wanetsi and Marheya study sites, Kruger National Park, South Africa. Different letters indicate significant differences ($P<0.05$). LSD = least significant difference of means at 5% level.

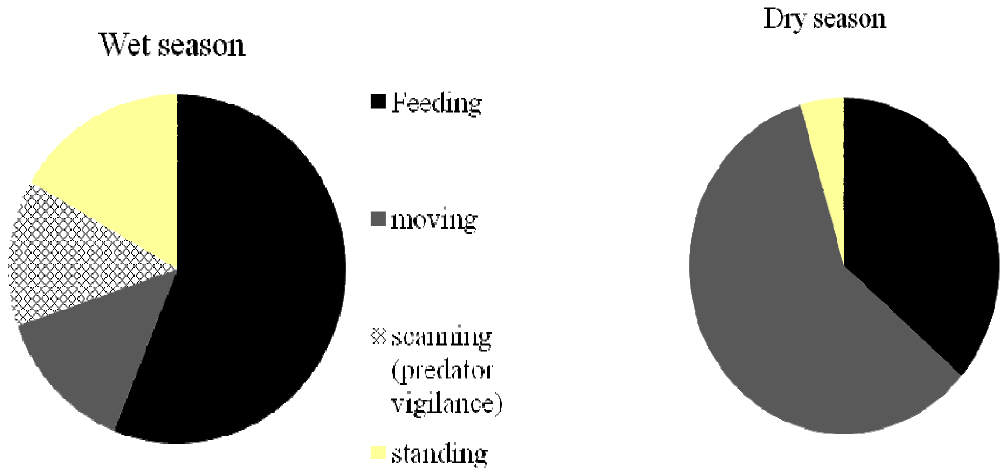

Figure 3.2 Impala behaviour (%) in a 3yr burning treatment plot for the wet and the dry season from Satara, N'wanetsi and Marheya study sites in the Kruger National park, n = 100.

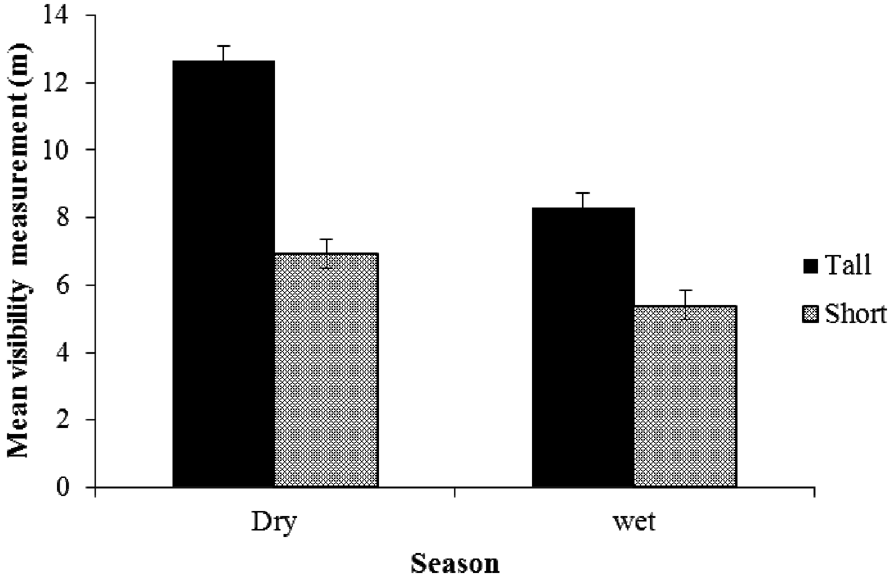

Figure 3.3 Mean (± se) visibility measurements of all herbivore species at the dry and the wet season (visibility in the dry season is significantly higher than in the wet season) combined for the control, new plot, 3yr and 1yr EBPs at Satara, N'wanetsi and Marheya study sites, Kruger National Park, South Africa. Tall represents 1.5 m and short represents 0.8 m eyesight height.

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Table 3.1. Mammalian herbivores (> 5kg) on the EBPs at Satara, N'wanesti and Marheya in the Kruger National Park, South Africa. The number of individuals of each species reported is based on the total observations (July 2009 – June 2010) for all study plots combined. Total biomass observed on the plots is calculated by multiplying the estimated per capita biomass by the number of individuals observed. * Biomass estimated for the average individual from each species (Skinner and Chimimba, 2005).

Herbivore species	Scientific name	Feeding guild	Number of individuals	Individual biomass (kg)*	Total biomass (tons)
African elephant	*Loxodonta africana*	Mixed	36	5700	205.2
Impala	*Aepyceros melampus*	Mixed	523	50	26.2
White rhinoceros	*Ceratotherium simum*	Grazer	27	2200	59.4
Cape buffalo	*Syncerus caffer*	Grazer	508	700	355.6
Burchell's zebra	*Equus burchelli*	Grazer	535	300	160.5
Waterbuck	*Kobus ellipsiprymnus*	Grazer	13	260	3.4
Blue wildebeest	*Connochaetes taurinus*	Grazer	173	250	43.3
Warthog	*Phacochoerus aethiopicus*	Grazer	46	80	3.4
Giraffe	*Giraffa camelopardalis*	Browser	25	1200	30.0
Kudu	*Tragelaphus strepsiceros*	Browser	36	250	9.0
Grey duiker	*Sylvicarpa grimmia*	Browser	2	15	0.03
Steenbok	*Raphicerus campestris*	Browser	35	10	0.4

Table 3.2 Correlations between herbivore distributions, for all species combined, and soil nutrients and vegetation structure and composition

	Herbivore density (ha^{-1})	p-value
Soil N (%)	-0.0871	0.7879
Soil Organic C (%)	0.3668	0.2408
Soil K (mg.kg^{-1})	0.1237	0.7016
Soil M (mg.kg^{-1})	-0.5374	0.0715
Soil P (mg.kg^{-1})	-0.0651	0.8407
Soil Ca (mg.kg^{-1})	-0.0023	0.9944
Tree density (ha^{-1})	0.1481	0.646
Tree height (m)	-0.1874	0.5597
Shannon' diversity index (H) of trees	0.2826	0.3735
Grass cover (%)	-0.4515	0.1407
Forb cover (%)	0.1422	0.6592
Shannon' diversity index (H) of grasses	-0.0338	0.9169
Shannon' diversity index (H) of forbs	0.2671	0.4014

Table 3.3 Correlations between herbivore distributions in the wet and the dry season, for grazing herbivores, and forage quality (grass digestibility, C, N and C:N) and quantity (plant biomass) for the wet (Jan 10 – Mar 10) and the dry (Apr 10 – Jun 10) season

	Wet season grazing herbivores (mean no. of dung piles)	Wet season p-value	Dry season grazing herbivores (mean no. of dung piles)	Dry season p-value
Digestibility (%)	0.3828	0.2193	0.128	0.6918
Grass tissue C:N	-0.0185	0.9545	-0.3402	0.2792
Plant biomass (kg/ha)	0.0311	0.9236	-0.4564	0.1358

Appendices

Appendix A: Dominant grass species selected for the forage quality measurements (grass tissue C:N and digestibility analysis) for each burning treatment on the selected EBPs from the three study sites in the Kruger National Park, South Africa.

Study site	Burning treatment	Grass species
Marheya	Control (unburned)	*Panicum coloratum*
		Digitaria eriantha
		Bothriochloa radicans
		Urochloa mosambicensis
		Panicum maximum
Marheya	New Plot	*Digitaria eriantha*
		Themeda triandra
		Bothriochloa radicans
		Panicum coloratum
		Eragrostis nindensis
Marheya	Triennial burned	*Panicum maximum*
		Urochloa mosambicensis
		Bothriochloa radicans
Marheya	Annual burned	*Bothriochloa radicans*
		Panicum coloratum
		Urochloa mosambicensis
N’wanetsi	control	*Panicum maximum*
		Panicum coloratum
		Digitaria eriantha

		Brachiaria deflexa
N’wanetsi	New plot	*Urochloa mosambicensis*
		Bothriochloa radicans
		Themeda triandra
N’wanetsi	Triennial burned	*Panicum coloratum*
		Bothriochloa radicans
		Themeda triandra
N’wanetsi	Annual burned	*Bothriochloa radicans*
		Tragus berteronianus
		Urochloa mosambicensis
Satara	Control	*Bothriochloa radicans*
		Digitaria eriantha
		Panicum coloratum
		Urochloa mosambicensis
Satara	New plot	*Themeda triandra*
		Panicum maximum
		Bothriochloa radicans
Satara	Triennial burned	*Digitaria eriantha*
		Panicum coloratum
		Bothriochloa radicans
		Themeda triandra
		Urochloa mosambicensis
Satara	Annual burned	*Panicum coloratum*

	Urochloa mosambicensis
	Bothriochloa radicans

Appendix B

Table 1: Study site and burning treatment abbreviations

Acronym	Study sites and associated burning treatments
MC	Marheya Control (unburned) plot
MN	Marheya New plot
M3	Marheya, triennial burnt plot
M1	Marheya, annual burnt plot
NC	N’wanetsi Control (unburned) plot
NN	N’wanetsi New plot
N3	N’wanetsi, triennial burnt plot
N1	N’wanetsi, annual burnt plot
SC	Satara, Control (unburned) plot
SN	Satara New plot
S3	Satara, triennial burnt plot
S1	Satara, annual burnt plot

Table 2: Grass species abbreviations for the CA ordination plot

Acronym	Grass species
Ariad	*Aristida adscensionis*
Aribar	*Aristida barbicollis*
Aricon	*Aristida congesta*
Botrad	*Bothriochloa radicans*
Bradef	*Brachiaria deflexa*
Cencil	*Cenchrus ciliaris*
Chlvir	*Chloris virgata*
Dacgic	*Dactyloctenium giganteum*
Digeri	*Digitaria eriantha*
Ennsco	*Enneapogon scoparius*
Eronin	*Eragrostis nindensis*
Erosup	*Eragrostis superba*
Hetcon	*Heteropogon contortus*
Pancol	*Panicum coloratum*
Panmax	*Panicum maximum*
Schpap	*Schmidtia pappophoroides*
Setinc	*Setaria incrassata*
Sorver	*Sorghum versicolor*
Thetri	*Themeda triandra*
Traber	*Tragus berteronianus*

Uromos	*Urochloa mosambicensis*

Table 3: Forb species abbreviations for the CA ordination plot

Acronym	Forb species
Acavil	*Acalypha villicaulis*
Achlep	*Achyropsis leptostachya*
Becob	*Becium obovatum*
Certri	*Ceratotheca trilobum*
Chamim	*Chamaecrista mimosoides*
Chaina	*Chamaesyce inaequilatera*
Comere	*Commelina erecta*
Compil	*Commicarpus pilosus*
Corasp	*Corchorus asplenifolius*
Crotvir	*Crotalaria virgulata*
Cuchir	*Cucumis hirsutus*
Cuczey	*Cucumis zeyheri*
Evoals	*Evolvulus alsinoides*
Gisafr	*Gisekia africana*
Helstr	*Heliotropium strigosum*
Hybenn	*Hybanthus enneaspermus*
Indpar	*Indigastrum parviflorum*
Ipople	*Ipomoea plebeia*

Jusfla	*Justicia flava*
Ociame	*Ocimum americanum*
Pavbur	*Pavonia burchellii*
Phybur	*Phyllanthus burchellii*
Phymad	*Phyllanthus maderaspatensis*
Phynum	*Phyllanthus nummulariifolius*
Sidcor	*Sida cordifolia*
Sidsca	*Sida scabrida*
Solpan	*Solanum panduriforme*
Tepnod	*Tephrosia grandiflora*
Teppur	*Tephrosia purpurea*
Tepsem	*Tephrosia semi-glabra*
Trarup	*Tragia rupestris*
Triter	*Tribulus terrestris*
Verfas	*Vernonia fastigata*

Table 4: Tree species abbreviations for the CA ordination plot

Acronym	Tree species
Acabor	*Acacia borleae*
Acanig	*Acacia nigrescens*
Acarob	*Acacia robusta*
Acator	*Acacia tortilis*
Baugal	*Bauhinia galpinii*
Bosfoe	*Boscia foetida*
Comher	*Combretum hereoensis*
Comimb	*Combretum imberbe*
Comhar	*Commiphora harveyi*
Comsch	*Commiphora schimperi*
Darmel	*Dalbergia melanoxylon*
Diccin	*Dichrostachys cinerea*
Ehrrig	*Ehretia rigida*
Gartra	*Garcinia transvaalensis*
Grebic	*Grewia bicolor*
Grehex	*Grewia hexamita*
Gymsen	*Gymnosporia senegalensis*
Lansch	*Lannea schweinfurthii*
Ormtri	*Ormocarpum trichocarpum*
Papcap	*Pappea capensis*
Pelafr	*Peltophorum africanum*

Phivio	*Philenoptera violacea*
Scebir	*Sclerocarya birrea*
Secvir	*Securinega virosa*
Zizmuc	*Ziziphus mucronata*

Table 5: Shannon' diversity (H) index of all grass species from the CA ordination analysis

Study site	Burning treatment	Shannon' diversity (H) of grass species
Marheya	Control (unburned)	2.18479
Marheya	New Plot	1.91895
Marheya	Triennial burned	2.08161
Marheya	Annual burned	1.28963
N’wanetsi	Control (unburned)	1.90041
N’wanetsi	New Plot	1.97938
N’wanetsi	Triennial burned	1.36836
N’wanetsi	Annual burned	1.52567
Satara	Control (unburned)	1.83913
Satara	New Plot	1.80945
Satara	Triennial burned	1.63251
Satara	Annual burned	1.70108

Table 6: Shannon' diversity (H) index of all forb species from the CA ordination analysis

Study site	Burning treatment	Shannon' diversity (H) of forb species
Marheya	Control (unburned)	2.5316
Marheya	New Plot	1.83348
Marheya	Triennial burned	2.47461
Marheya	Annual burned	1.7168
N’wanetsi	Control (unburned)	2.33225
N’wanetsi	New Plot	2.27229
N’wanetsi	Triennial burned	0.50944
N’wanetsi	Annual burned	1.33591
Satara	Control (unburned)	2.22798
Satara	New Plot	2.48549
Satara	Triennial burned	2.16895
Satara	Annual burned	1.86658

Table 7: Shannon' diversity (H) index of all tree species from the CA ordination analysis

Study site	Burning treatment	Shannon' diversity (H) of tree species
Marheya	Control (unburned)	1.50842
Marheya	New Plot	1.2369
Marheya	Triennial burned	1.3001
Marheya	Annual burned	1.63222
N'wanetsi	Control (unburned)	1.67421
N'wanetsi	New Plot	1.73498
N'wanetsi	Triennial burned	0.87583
N'wanetsi	Annual burned	1.27182
Satara	Control (unburned)	1.86541
Satara	New Plot	1.64556
Satara	Triennial burned	0.96107
Satara	Annual burned	1.67163

APPENDIX C: Herbivore behaviour recorded from the selected EBPs from the three study sites in the Kruger National Park, South Africa.

Behaviour #	Code	Behaviour
1	b	Browse
2	g	Graze
3	m	Moving
4	p	Scanning (predator vigilance etc.)
5	r	Resting
6	S	Socialising
7	u	Foraging, unknown forage
8	x	Behaviour unknown, view obscured
9	j	Self grooming
10	l	Standing (ruminating)
11	d	Drinking
12	st	Standing (non-ruminating)
13	n	nursing