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FIRE-GRAZER INTERACTIONS IN A HIGHVELD GRASSLAND IN SOUTH AFRICA

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A Dissertation submitted to the Faculty of Science in fulfilment of the requirements for the Master of Science degree.

In

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Johannesburg

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Supervisor: Prof. Sally Archibald

PREFACE

The experimental work described in this dissertation was carried out in the School of Animal, Plants and Environmental Sciences, in the University of the Witwatersrand, Johannesburg, South Africa, from March 2015 to March 2017, under the supervision of Professor Sally Archibald (also in the School of Animal, Plants and Environmental Sciences, University of Witwatersrand, Johannesburg, South Africa). These studies represent the original work of the author and have not been submitted in any form for any degree or diploma at any University unless stated otherwise.

Signed:

F. Skhosana (MSc candidate)

Signed:

Prof. Sally Archibald (Supervisor)

PLAGIARISM DECLARATION

I Felix Skhosana (student number: 544258), a student registered for an MSc degree by Dissertation in the year 2015 to 2017, I hereby declare that:

The work presented in this dissertation is my own, unaided work and it has not been submitted before for any degree or examination at any other University except where I have explicitly indicated otherwise. I understand that the University may take disciplinary action against me if there is a belief that I failed to acknowledge the source of the words in my dissertation.

Signature:

Date: 06 July 2017

ABSTRACT

Fire is known to affect spatial patterns of grazing by altering the amount and quality of forage. Animals select the post-burn green flush that remains palatable until the grass recovers its biomass. How quickly the grass regrows depends on the rainfall and grass growth rates, and also grazing intensity. Theoretically, highly concentrated grazing can maintain short (relatively more palatable) grasslands throughout a growing season. Therefore this study aimed at; i) determining how long different grazer species were attracted to the burn, and whether this increased grazing pressure (as a result of concentrating grazers on a small burnt patch) maintained a short, palatable grass sward throughout the growing season, ii) investigating the long-term impacts of herbivore attraction to small burns on grass community and landscape function in a Highveld grassland. We therefore monitored grazer utilization of an experimentally applied small (5ha) burnt patch using dung counts and camera traps, and also measured the structural changes of the burnt patch over a period of 12 months. To test whether this process of attraction to small burns could have long-term impacts on grass community composition and landscape function we quantified species composition, infiltration rates, soil compaction, soil moisture, and ANPP in another landscape which had received 10+ years of small annual burns (a firebreak). A novel finding was that indeed grazers especially the short-grass specialist stayed on the burn and kept the grass short (<10cm) for the duration of the study post fire: the burn only treatment on the 5ha burn recovered its biomass within 2 months of the first rains. This result was due to the fact that it was a drought year with half the normal rainfall (and lower grass regrowth rates). However, the long-term study indicated that the attractive effect of small fires in this ecosystem alters both community composition and ecosystem properties. The firebreak had more bare ground and less water infiltration than the surrounding grassland – but was more diverse and had higher grass productivity. It also continued to attract the short-grass specialist species (blesbok, wildebeest and hartebeest). This counter-intuitive result indicates that perhaps these grasslands are not as severely degraded as we think. This study therefore, showed that coupling small burns with appropriate grazer species has a great potential for creating palatable grazing “hotspots”, in sourveld grassland without obvious damage to ecosystem function.

ACKNOWLEDGEMENTS

Firstly I would like to thank the National Research Foundation (NRF) and the Partnerships for Enhanced Engagement in Research (PEER) for funding this project. Most importantly as well, I would like to express my deepest gratitude to my Supervisor, Professor Sally Archibald for her tremendous ideas as well as her everlasting patience and presence whenever I needed help. With her vast knowledge not only in Ecology I must say all her ideas, guidance and advices were very inestimable and constructive. In the same spirit of gratitude I would like to applaud Hannelie Coetzee for collaborating with us in this project and coming up with the idea to burn the patch in the form of an artwork. The 5ha image named “Benko & Eland” (shown in Chapter 2) grew very famous over media and, further won us an award at the 19th Annual BASA Awards. Burning this image was also made possible by the team of quantity surveyors (Kirchhoff Surveyors) and another team from Working on Fire, to whom I’m grateful.

In extending my gratitude, this project would never been possible if it wasn’t for the owner of Kromdraai Nature Reserve (Benji Liebermann) and the manager of the farm (Stephan du Toit) who gladly opened their gates for us to run our experiments in their farm. Stephan du Toit also provided us with rainfall data and as well as the relevant information about the fire history and the grass species occurring at the site. Michael Mulaula (works at the farm) was always there to open the gate for me every morning when I came in and in the evening when I left after collecting data. He always welcomed me with a smile and he never complained even once.

I’m further grateful for all the help I got during my data collection at the site. For that and simultaneously keeping me in company, I would like to thank my supervisor again, my colleague and friend (Alekzandra Scewczuk), my girl-friend (Norin Sibanda) and two of my friends (Khayelihle Jamela and Mthokozisi Moyo). Alekzandra is further acknowledged for willingly sharing with me her data on NPP and grazer presence used in Chapter 3. Other important ideas around this project were further obtained from these iconic ecologists; Mr. Gareth Hempson, Miss Swanni Alvadro, Prof. William Bond, Dr. Suzanne Vetter and Dr. Jason Marshal. For that I would like to extend my gratitude. Finally, I would like to thank my family (both my parents and siblings) and friends for all their emotional support during the entire period of my study.

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1 Chapter 1: GENERAL INTRODUCTION

1.1 Literature review

Fire and herbivory are two important disturbances or primary consumers in grassland ecosystems in the world (Collins and Smith 2006). They have been documented to play a vital role in maintaining biomes that are ecologically and economically important such as savannas and grasslands (Scholes and Archer 1997). The importance of grasslands lies in the fact that they occupy up-to 26% of the earth’s land of which 80% of it is utilised for agricultural purposes such as livestock and crop farming which boost the global economy (Boval and Dixon 2012). Moreover, grasslands play a crucial role in being biodiversity reserves and in alleviating the emissions of greenhouse gasses by being a potential carbon sink (Boval and Dixon 2012). There is much evidence that savannas and grasslands would become encroached with woody species if it were not for the frequent fires and herbivory which keep woody biomass low (Trollope 1974; Trollope 1980; Scholes and Archer 1997; O’Connor and Crow 1999; Ward 2005; Wigley *et al.* 2009; Staver *et al.* 2009). However, from here onwards I will be focusing on grazing not browsing. Many studies (Sala 1988; Barnes 1990; Anderson and Briske 1995; Collins *et al.* 1998) on the effect of fire and grazing on grassland communities have focused on these two disturbances separately with just a few studies (Fuhlendorf and Engle 2004; Archibald *et al.* 2005; Sensenig *et al.* 2010) paying attention on the combined effect of fire and grazing, in this study referred to as fire-grazer interactions. This fire-grazer interaction is as a result of pyric herbivory, which is defined as grazing driven by fire (Fuhlendorf *et al.* 2009; Allred *et al.* 2011).

1.2 Fire-grazer interactions

In some senses fire and grazing could be seen as competing with each other for the grassy biomass, but the interactions between these two consumers are more complex than this. Several studies have documented that fires affect the movement of herbivores across the landscape by attracting animals to more recently burnt areas (pyric herbivory (Coppedge and Shaw 1998; Archibald and Bond 2004; Archibald *et al.* 2005; Fuhlendorf *et al.* 2009; Sensenig *et al.* 2010; Allred *et al.* 2011). As a result of this pyric herbivory, soon after a fire event, grazers will move onto the recently burnt patches due to the new growth which is more nutritious and palatable (in this study, more preferred) relative to the patches with long time since fire (Tomor and Owen-Smith 2002; Allred *et al.* 2011; Augustine and Derner 2014). Whether this concentrates or disperses the animals depends on the size of the fire and the density of the herbivores (Archibald and Bond 2004; Archibald 2008). It appears that ruminants such as impalas are more attracted to post-burn grassland than hindgut fermenters such as zebras (Wilsey 1996; Augustine and Derner 2014). For ruminants, this selection for recently burnt areas is even more conspicuous in those of smaller body sizes (10 – 500 kg) compared to those of larger body sizes weighing more than 500 kg (Sensenig *et al.* 2010; Augustine and Derner 2014). This can be explained by the trade-off between forage quality and quantity, since the recently burned areas have low forage quantity but high forage quality and vice versa for the areas with long time since fire (Tomor and Owen-Smith 2002; Augustine and Derner 2014). Therefore, small ruminants with high metabolic requirements (Sensenig *et al.* 2010) need to select areas with high forage quality. Moreover, differences in muzzle width can also affect whether herbivores make use of very short grass (Arsenault and Owen-Smith 2008). Therefore, the determining factor is not simple as body size but more related to mouth shape and other factors such as metabolic demands (Arsenault and Owen-Smith 2008), and wildlife situations herbivore use of the burned area could also relate to fear of predation, with post-burn landscapes offering better visibility (Allred *et al.* 2011). Therefore a wide variety of herbivore types make use of post-burn landscapes.

In contrast, grazing affects fire by removing grass biomass that would otherwise be fuel (Fuhlendorf and Engle 2004; Leonard *et al.* 2010).The effect of grazing on fire is less complex because it does not involve a behavioural switch and is based purely on how grazing affects the amount and continuity of the fuel such that once grazers have reduced the fuel below the level where fire can spread, then grazing limits fire by forming “firebreaks” within the grassland (Leonard *et al.* 2010).

After the fire, the intensity of grazing on a patch will affect how rapidly grass biomass regrows, which further affects the fuel for future fires. The high utilization of recently burnt patches relative to the unburnt ones by grazers can result in a negative feed-back such that there will not be enough fuel for the next fire event hence reducing the probability of burning in the future (Augustine and Derner 2014). In contrast, the unburnt patches, which have been relieved of grazing pressure due to animals moving into the burns, accumulate fuel and are more likely to burn in future (Fuhlendorf and Engle 2004). As a result of these spatially discrete fires causing focal grazing to be shifted to other patches overtime, the landscape can be described as a shifting mosaic (Fuhlendorf and Engle 2004). These spatiotemporal interactions between ungulate grazers and fire are potentially important drivers of the changes in composition, structure and functioning of many grassland or rangeland ecosystems globally (Archibald *et al.* 2005; Murphy and Bowman 2007; McGranahan *et al.* 2012). Thus fire has been used as a management tool in both the United States of America (Teague and Dowhower 2003; Fuhlendorf and Engle 2004; Fuhlendorf *et al.* 2009; Winter *et al.* 2012) and southern Africa (Booysen 1967; Willis and Trollope 1987; Brockett *et al.* 2001; Gebeyehu and Samways 2003) to create rotational grazing systems where animals are constantly moved from place to place so that they never graze one patch of land too heavily. Furthermore, the level at which herbivores select and forage on recently burnt patches over unburnt patches plays a crucial role on patch level vegetation structural heterogeneity (variance) in grassland ecosystems (Fuhlendorf and Engle 2004; Winter *et al.* 2012; Augustine and Derner 2014). An increase in heterogeneity across the landscape has been shown to be an important variable critical to some rangeland animals (e.g. birds that need both short and long grassland to complete their life-histories) and the structure and functioning of grassland ecosystems (Roth 1976; Fuhlendorf and Engle 2004; Allred *et al.* 2011).

1.3 The Sourveld grassland

There are various models which predict under which conditions grazed ecosystems will become degraded, versus sustaining high productivity (Díaz *et al.* 2007). However, discussing what degradation means is really a complicated issue because there has been some heated arguments around this and no one is agreeing on one definition. Therefore, in this study I shifted the focus to landscape functioning as a way to get around degradation (even though I referred to bareground, soil moisture, infiltration rates and soil compaction as degradation measures). According to Tongway and Hindley (2004) landscape function is defined as the ability of the landscape to absorb and retain critical elements (especially abiotic factors such as soil moisture and nutrients) to plants and ultimately the maintenance of plant productivity which further benefit animals as well as hindering negative impacts such as soil erosion (increase plant cover and reduction in bareground). Some theories predict that high rainfall sites are less likely to be poor in landscape functioning because grasses can regrow lost biomass quickly (Milchunas *et al.*

1988) whereas other authors theorise that high rainfall areas are more likely to be poor in landscape functioning because the grasses there are inherently less palatable (Coley *et al.* 1985). By "poor landscape functioning" we are simple referring to a landscape prone to degradation (eroded landscape with low soil nutrients and low productivity). In South Africa, this distinction is summarised by the terms "Sourveld" and "Sweetveld" (Trollope 1980; Trollope 1990). Sourveld occurs in cool, wet and infertile (due to leaching of nutrients) highlands where carbon assimilation is high relative to nutrient supply, whereas Sweetveld occurs in warm, arid and fertile lowlands where the nutrient supply is high relative to carbon assimilation (Scholes 1990; Ellery *et al.*1995; Hardy *et al.*1997).

Furthermore, Sourveld and Sweetveld grasslands also differ functionally and in species composition (Ellery *et al.* 1995). The functional differences are that grass forage in Sourveld does not retain enough nutrients in the winter to sustain grazers due to the relatively higher C:N ratio of the grass (Hardy *et al.* 1997). In the Sourveld therefore, grass is only palatable early in the growing season, or when regrowing after fire (Hardy *et al.* 1997). Hence, the indirect impact of fires on grazing is expected to be different in the Sourveld relative to the Sweetveld. I propose that fires will impact grazing more on the Sourveld because: **a)** the surrounding grass is less palatable (i.e. relatively more attractive resource to grazers thereafter) and **b)** it is more likely that the grass will re-sprout during the winter as there is usually more residual soil moisture (Hardy *et al.* 1997). According to Ellery *et al.* (1995) these two distinct types of grasslands are also characterised by different grass species composition, although some species occur across both environments (Table 1.1). This distinction between Sourveld and Sweetveld is similar to findings of Visser *et al.* (2012) who showed that arid areas are dominated by plants in the grass sub-clades Chloridoideae and Aristideae, whereas mesic areas with high fire are dominated by Andropogoneae. However, neither of these perspectives takes into account local-scale changes in grass communities within a landscape. Imposed on these large-scale environmentally controlled patterns, the compositional and functional character of a grassland can depend strongly on the type and pattern of herbivory it has experienced.

Table 1.1: Grass species composition occurring at two distinct grassland environments (Sourveld and Sweetveld) and those co-occurring at both grasslands according to Ellery *et al.* 1995.

Sourveld grass species	**Intermediate species**	**Sweetveld grass species**
Allopterosis semialata	*Themeda triandra*	*Digitaria eriantha*
Andropogon schirensis	*Brachiaria serrata*	*D. tricholaenoides*
Andropogon appendiculatus	*Brachiaria nigropedata*	*Eragrostis obtusa*
Aristida congesta	*Setaria sphacelata*	*Anthephora pubescens*
Aristida diffusa	*Microchloa caffra*	*Panicum coloratum*
Aristida adscensionis	*Heteropogon contortus*	*Paspalum scrobiculatum*
Aristida bipartita	*Melinis repens*	*Tetrachne dregei*
Aristida junciformis	*Melinis nerviglumis*	
Aristida stipitata	*Diheteropogon amplectens*	
Aristida tranvaalensis	*Digitaria monodactyla*	
Cymbopogon plurinodis	*Eragrostis curvula*	
Diheteropogon filifolius	*Eragrostis capensis*	
Eragrostis plana	*Eragrostis chloromelas*	
Eragrostis sclerantha	*Eragrostis palens*	
Hyparrhenia hirta	*Eragrostis racemosa*	
Panicuum decklonii	*Eragrostis superba*	
Schizachyrium sanguineum		
Sporobolus africanus		
Sporobolus pyramidalis		
Sporobolus fimbriatus		
Trachypogon spicatus		
Tristachya remannii		
Tristachya leucothrix		

In Southern African rangeland literature, grasses are classified into three categories; Decreaser species, Increaser I species or Increaser II species (Teague *et al.* 1981; Trollope *et al.*

1989; Trollope *et al.* 1990; Trollope 1990). Decreaser species are the species of grasses and forbs which tend to decrease when the veld is under or over utilised, whereas, the Increaser I and Increaser II species are grass and forb species which increase when the veld is underutilised and over-utilised respectively (Trollope *et al.* 1989). While this classification encompasses local-scale variability related to grazing and fire pressure, it does not directly relate to plant traits or functional responses: for example, members of the *Aristida* genus are increaser II species, so are often termed "grazing tolerant" when in fact they are just not palatable, so not preferred by grazers. Generally increaser II species are considered undesirable, but there are some species that increase under heavy grazing which are very good forage quality as well as being highly grazing tolerant. Therefore, one of the problems with the classification is that palatable and unpalatable grasses get placed in the same category yet they have very different ways of dealing with heavy grazing. Therefore, this categorisation does not help us to distinguish when heavy grazing results in a less productive state versus a highly productive grazing lawn state.

Grazing lawns are defined as communities of short-statured grasses whose persistence and spread is promoted by grazing (Hempson *et al.* 2014). The term was first used by Lock (1972) referring to Hippopotamus (*Hippopotamus amphibious*) grazing lawns. McNaughton (1984) further described the mechanisms in which grazing lawns were created and maintained by heavy grazing. Grazing lawns are a very common natural occurrence in many grassland ecosystems (McNaughton 1984; Archibald *et al.* 2005; Hempson *et al.* 2014) and grasses occurring in grazing lawns have traits which allow them to both promote grazing (palatability) and to persist under heavy grazing (grazing resistance) (Cingolani *et al.* 2005). Therefore in terms of the Briske's (1996) grazing ecological strategies lawn grass species tend to follow an architectural resistance strategy: i.e. they survive in overgrazed areas with their architectural characteristics that allow them to avoid too intense herbivory (holding leaf material close to the ground and growing in a prostate architecture) (Hempson *et al.* 2014).

There is some disagreement in the literature about whether grazing lawns are 1) systems where the grass is kept short and productive by grazing (but the same grass species as in the surrounding tall grass areas) or 2) systems with a distinct grass community tolerant of and adapted to heavy grazing (more discussions of this on Arnold *et al.* (2014)). Some of the classic grazing lawn examples (e.g in the Serengeti) are probably an example of definition 1 (above) but changes in species composition are likely to be more permanent, and result in increased overall biodiversity (McNaughton 1984; Milchunas *et al.* 1989; Du Toit and Cumming 1999).

There is much debate on the conditions which allow the development of grazing lawns. Many lawns are associated with features such as nutrient hotspots or water points which act to attract and concentrate grazers (Stock *et al.* 2010; Arnold *et al.* 2014; Hempson *et al.* 2014). It is theoretically possible however (Archibald 2008) for heavily grazed lawn patches to develop in a uniform landscape simply through positive feedbacks between short grass and palatability. That is, grazing lawns can result if the grazers keep coming back to the same patch (Archibald 2005).

1.4 Dissertation goals and structure

This thesis aimed at assessing; i) the short-term (seasonal) impacts of small burns on grazers and grass community structure by determining how long different grazer species were attracted to the burn, and whether this added grazing pressure maintained a short, palatable grass sward throughout the growing season (in Chapter 2), and ii) the long-term (decadal) impacts of herbivore attraction to small burns on grass community and landscape function in a Highveld grassland (in Chapter 3). Even though the effect of grazing on grasslands has been well-documented, there are several contradictory models about what type of grass communities result from intensive grazing – in particular, under what conditions it results in degradation versus a highly reproductive system. Therefore, the third chapter has a section about the long-term impact of fire and grazing (combined) on grass productivity.

This dissertation is structured in a way that the first chapter entails the main introduction of the studies done and its literature review also gives a sufficient background to the study. Following it is the description of the study site, since the sites of the two data chapters were both located inside one big conservation area (Kromdraai Nature Reserve). The second chapter is a data chapter, addressing the first (i) part of the aim which looks at the short-term (seasonal) impact of a small burn (5ha) on grazer movements and grass community structure by determining how long different grazer species were attracted to the burn, and whether this added grazing pressure maintained a short, palatable grass sward throughout the growing season. The third chapter is also a data chapter, addressing the second (ii) part of the aim – looking at the long-term (decadal) impact of herbivore attraction to small burns on grass community and landscape function in a Highveld grassland. Lastly, the fourth chapter gives an overall discussion and conclusions to all the chapters combined.

1.5 Describing the study site

Both studies for chapter 1 and 2 were done at Kromdraai Nature Reserve (25˚58ˈ40ˈˈS, 27˚46ˈ43ˈˈE) in the Highveld, north of Johannesburg (Figure 1.1). The farm (within the Cradle of Humankind) covers an area of 1200ha with an altitude of about 1600m. The landscape is characterized by soils derived from ancient granitic geologies with rocky dolomitic outcrops (Berger *et al.* 2003; Bamford *et al.* 2010). The Cradle area receives high annual summer rainfall of about 650 - 750 mm (Figure 1.2; Avery 2001; Bamford *et al.* 2010) and experiences warm conditions during summer and is colder with frost during winter seasons (Avery 2001; Bamford *et al.* 2010). The temperatures range from -12ºC (during winter) to 39ºC (during summer) with an average of 16 ºC (Bamford *et al.* 2010).

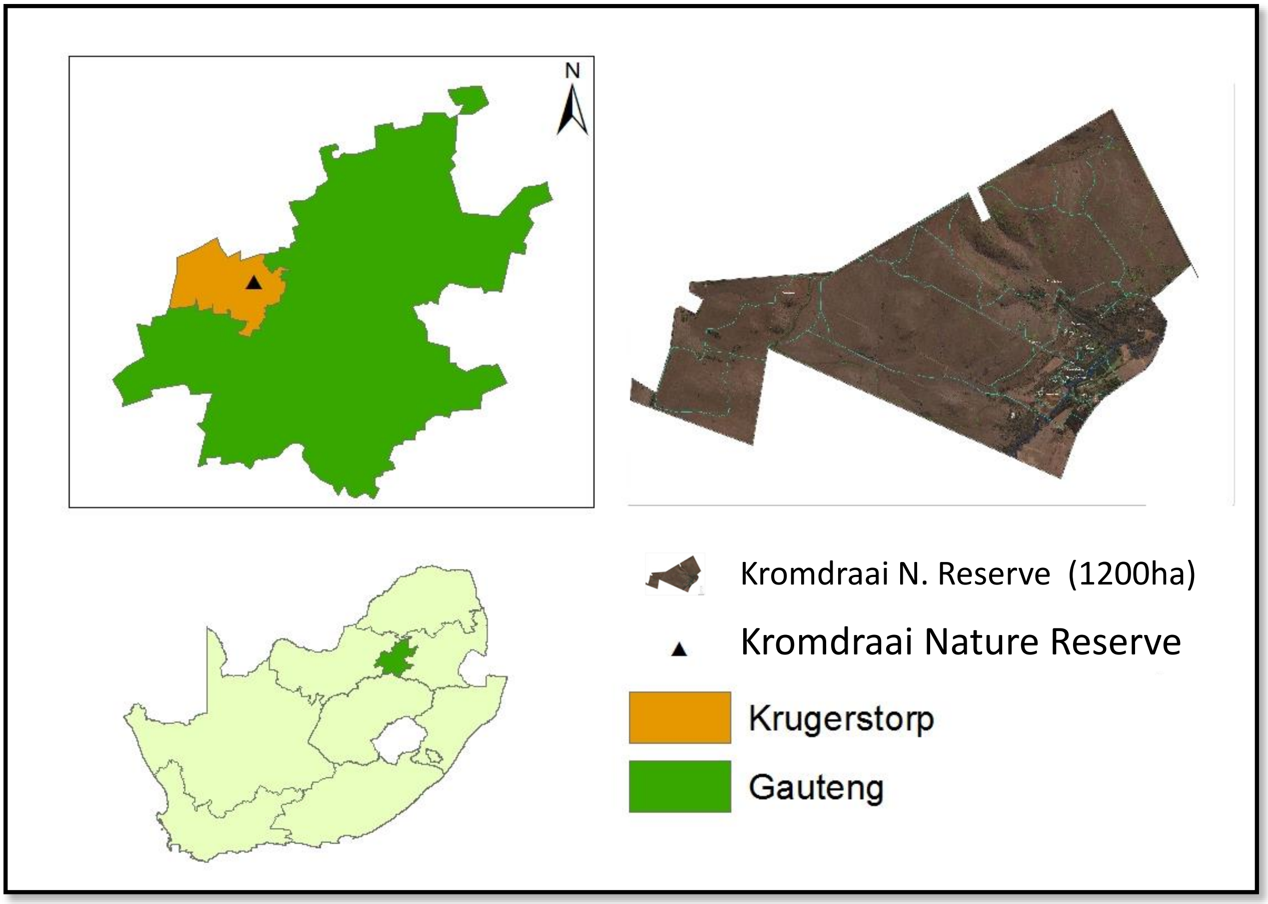

Figure 1.1: Map showing the 1 200ha study site, Kromdraai Nature Reserve (Nirox N. Cons.) located towards the edge of Krugersdorp within the Cradle of Humankind area.

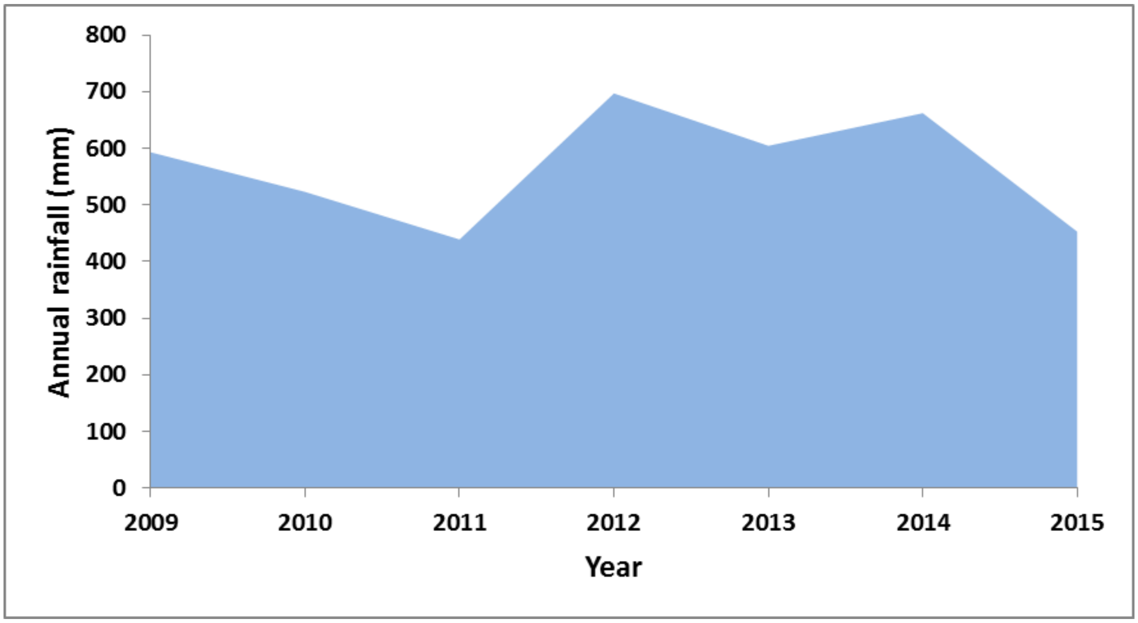

Figure 1.2: Annual rainfall recorded at the study site (Kromdraai Nature Reserve) for the past 6 years by the farm manager (Stephan du Toit).

1.6 Flora and fauna

The vegetation within the Cradle of humankind is characterised by mainly grasslands with high species richness followed by forbs and pockets of trees and shrubs (Mucina and Rutherford 2006; Figure 1.3). The most common grass species in the area are *Themeda triandra*, *Brachiaria serrata*, *Aristida spp*., *Setaria spp*., *Eragrostis spp*., and *Cymbopogon caesius* (Mucina and Rutherford 2006; Personal Obs.). Forb species comprise mostly *Helichrysum spp*., *Richardia brasiliensis*, *Oxalis corniculata* and *Hermannia depressa* (Personal Obs.). Woody species include *Ziziphus zeyheriana*, *Stoeb vulgaris*, *Acacia* species and *Berkheya annectens* (Mucina and Rutherford 2006; Personal Obs.)

My experiments (labelled “New-burn” for Chapter 2, and “Firebreak” for Chapter 3) were set up on a west – facing slope on the boundary of the park (Figure 1.3). The first site (“New-burn) was surrounded on both sides by firebreaks (for Chapter 3) that had been burned annually in April/May for at least the last 10 years (Stephan du Toit… pers com).

Figure 1.3: The vegetation at the studying site (Kromdraai Nature Reserve). The area labelled "New burn" with some white markings on the ground is where the experimental 5ha burn was implemented (more details on ch. 2). The area labelled "Firebreak" is where the sampled firebreak ran vertically down the slope (more details on ch. 3).

The 1200ha farm was occupied by different ungulate species of different population sizes and different feeding guilds such as grazers, mixed feeders and browsers all adding to a total of 256 individual ungulates (Table 1.2). In total the grazer biomass density on the 1200ha farm was 21.79kg/ha whereas the total mixed feeder and browser densities were 2.23kg/ha and 5.01kg/ha, respectively – making this study more appropriate at looking at grazers and mixed feeders than browsers. The average body mass (kg) for each grazer species used in the following two chapters (Chapter 2 and 3) for calculating herbivore biomass (kg/km^2) was obtained from literature (Table 1.2).

Table 1.2: Herbivore species and their population sizes found at the study site (Kromdraai Nature Reserve). Their feeding type or guild as well as their average body mass (kg) was obtained from literature for use in herbivore biomass calculations in chapter 2 and 3.

Herbivore species	**Population size at site**	**Feeding guild**	**Av. body mass (kg)**	**References**
blue wildebeest (*Connochaetes taurinus*)	35	Grazer	210.1	(Perez-Barberia & Gordon 2005)
zebra (*Equus burchelli*)	25	Grazer	280.9	(Perez-Barberia & Gordon 2005)
red hartebeest (*Acelaphus buselaphus*)	25	Grazer	130.0	(Perez-Barberia & Gordon 2005)
waterbuck (*Kobus ellipsiprymnus*)	24	Grazer	212.0	(Perez-Barberia & Gordon 2005)
blesbok (*Damaliscus pygargus*)	23	Grazer	53.0	(Melton 1978)
warthog (*Phacochoerus africanus*)	20	Grazer	73.5	(Stock *et al.* 2010)
impala (*Aepyceros melampus*)	42	Mixed	52.0	(Demment 1982; Stock *et al.* 2010)
gemsbok (*Oryx gazella*)	3	Mixed	150.0	(Melton 1978)
bushbuck (*Tragelaphus scriptus*)	15	Browser	40.4	(Perez-Barberia & Gordon 2005)
grey duiker (*Sylvicapra grimmia*)	10	Browser	17.0	(Perez-Barberia & Gordon 2005)
mountain rhebuck (*Pelea capreolus*)	7	Browser	28.0	(Melton 1978)
kudu (*Tragelaphus strepsiceros*)	25	Browser	217.5	(Pettorelli *et al.* 2009)

2 Chapter 2: SHORT-TERM IMPACTS OF FIRE AND GRAZER INTERACTIONS IN A HIGHVELD GRASSLAND

2.1 Introduction

In many grassland ecosystems fire plays a vital role in the ecosystem functioning of many types of grasslands through altering soil nutrient allocation, herbaceous structure and composition, habitat and forage availability for grassland species such as insects and birds and also forage quality and quantity for herbivores (Tscharntke and Greiler 1995; Kopij 2001; Little *et al.* 2013).

The response of grasslands to different fire regimes tend to depend both on the type of fire, and the amount of rainfall experienced by different grasslands. For instance, frequent fires on high rainfall grasslands have a great potential in changing the structure and composition of those grassland communities to tall and fast growing grasses that are highly flammable but intolerant to grazing (Archibald *et al.* 2005). The effect however differs on low rainfall short grasslands such that frequent fires can negatively affect the functioning of the landscape (in terms of high bare ground and soil erosion) (Johansen *et al.* 2001). Other important considerations in implementing prescribed fires are differences in time of the burn and the size of the area burnt. Unlike fires later in the dry season, fires early in the dry season are characterized as low intensity fires as the majority of the herbaceous layer still retains moisture from the previous wet season (Liedloff *et al.* 2001). Fire of this type generally burns in a patchy manner (also due to some of the uncured fuels especially at the bottom of the tussocks) and having less effect on the vegetation of the following year (Williams *et al.* 1999). Burns later in the dry season (when the herbaceous layer is completely dry) burns more intensely therefore affecting even the fresh buds hid by the tussocks waiting to shoot after the fire (Williams *et al.* 1999). Therefore, as a consequence, cooler fires in the early dry season has a greater impact at attracting grazers to the sporadic green flush causing focal grazing especially when applied on a small patch of land within the landscape (Archibald et al. 2005; Savadogo *et al.* 2007). Burning a small patch of land significantly draws grazers from the rest of landscape to that particular area whereas burning the entire area has less effect on grazer movement as grazing remain dispersed across the landscape (Archibald and Bond 2004). Therefore, fire has a strong effect in altering grazing behaviour and in-return, grazing alters the intensity and extent of future fires such that a burnt area has low potential of burning the following year as compared to the unburnt area with accumulated fuel load (Fuhlendorf and Engle 2004). This therefore favours rotational burning of small plots along the landscape resulting in a shifting mosaic of different types of patches unique in plant species composition and community structure across the landscape (Fuhlendorf and Engle 2004; Fuhlendorf *et al.* 2006; Fuhlendorf *et al.* 2009; Winter *et al.* 2012; Novellie and Gaylard 2013).

The shifting mosaic in grassland landscapes can be created through rotational grazing with the sole purpose of improving plant community composition and productivity across the landscape by forcing animals to relinquish preference (Briske *et al.* 2008). Moving grazers from a certain patch to another patch, usually barricaded by fencing allows the previous patch to be rested, therefore increasing productivity by ensuring that key plant species on a grazed-open patch capture sufficient resources (such as water, light and nutrients) for growth and photosynthesis to be efficiently foraged on by herbivores when they return (Briske *et al.* 2008). Moreover, the implementation of rotational grazing by concentrating grazers in one small patch through fencing or through increasing stock densities is to reduce grazer selectivity and consequently overcome patch grazing or small-scale heterogeneity (Briske *et al.* 2008), and prevent the loss of grazing-sensitive species. However, other scientists argue that the effect of rotational grazing on defoliation patterns seem to be weak even in small scales of normal paddocks of less than 20ha or 5ha (Bailey *et al.* 1996; Teague and Dowhower 2003). They argue that even in homogenous systems grazers continue to be selective, which is a something that the implementation of small fires can bring a solution to by manipulating grazers to graze a small burnt patch with less selectivity.

Since Highveld grasslands are generally characterized by high rainfall (Wakeling *et al.* 2010), early dry season burns seem to have less negative effects than late dry season burns on both annual and perennial grasses and forbs (Everson *et al.* 1985; Savadogo *et al.* 2007). The annuals survive the effects of fire through growing and reproducing rapidly during the growing season (due to adequate moisture) and by the early dry season their seeds would already be on the soil (Russell-Smith *et al.* 2001). Therefore, burning the dry and dying plants after seed set has no effect on the survival of these annual species. On the other hand, perennial grasses survive fire by forming dense tussocks, protecting the buds located below ground (Russell-Smith *et al.* 2001). As the dry season approaches, most of the tiller leaves and the stems die and become dry and susceptible to burning, so that the protected buds can quickly shoot in a period of days to few weeks after the fire (Russell-Smith *et al.* 2001). These tussocks however are not completely immune to fire depending on the size and the frequency of the fire, as well as the grazing pressure by herbivores. Frequent intense fires and intense grazing has a great potential in reducing the size of the tussocks which then reduces the protection of the buds (Brown and Stuth 1993; Russell-Smith *et al.* 2001). As an alternative, some tufted perennials such as *Cymbopogon* species may rely on their higher seed set to counteract this effect (Veenendaal *et al.* 1996). Moreover, burning the herbaceous fuel tends to release the nutrients at the soil surface (Snyman 2003), which can later be used by the regrowth, even though most of the nutrients eventually become susceptible to leaching later in the rainy season(Scholes 1990; O'Reagain and Owen-Smith 1996; Wakeling *et al.* 2010). Linking this to the soil moisture still residual early in the dry season creates a conducive environment for the green flush (preferred by herbivores), which supports the idea of implementing early low intensity winter burns for both conservational and management strategies.

The implementation of these small (discontinuously spread) early dry season burns also causes grazing and nutrient allocation to be patchily distributed across the landscape. Herbivores with high metabolic requirements (requiring high forage quality) such as most ruminants and small mammals (Sensenig *et al.* 2010; Augustine and Derner 2014) will choose to select for green flush (Wilsey 1996; Archibald *et al.* 2005), at the same time dropping their dung on those areas. As a result of small burns and discrete dropping of dung and the nutrient allocation across the landscape will also be only sequestered in those areas. Therefore, as opposed to large landscape fires, these interactions and processes between small fires and grazing and nutrient allocations result in heterogeneity across the landscape (Fuhlendorf and Engle 2004). Many studies have documented that the structural heterogeneity (short vs. tall grass) as a result of patchy or discontinuous small burns followed by grazing by ungulates has a strong effect on the richness and diversity of grasses and consumers such as insects and birds (Nagel 1973; Anderson *et al.* 1989; Tscharntke and Greiler 1995; Swengel 2001; Fuhlendorf *et al.* 2006; Isacch and Cardoni 2011; Little *et al.* 2013; Fuhlendorf *et al.* 2017).

In terms of plants we learnt in the previous chapter that grazing stimulates diversity and productivity, which raises the idea that the interaction of fire with grazing further increases diversity and heterogeneity across the landscape. Moreover, plant richness is recognised as a strong indicator of biodiversity both at local and regional scale, of-which its maximization is often crucial (Cingolani *et al.* 2010). The taxonomic richness of a whole region or management landscape is termed gamma diversity and it can be further divided and narrowed down to beta and alpha diversity (Cingolani *et al.* 2010). Beta diversity is therefore defined as the variation in species composition among different sites whereas, alpha diversity is defined as the number of species present at a single site (Cingolani *et al.* 2010; Poggio *et al.* 2010). Therefore based on these definitions patch-level (alpha) diversity might actually decrease due to the homogenous structure within burnt small areas yet contrasting patches (beta diversity) with different time since disturbance increase in diversity and ultimately an increase in landscape (gamma) diversity. According to Panzer and Schwartz (1998), there is a strong correlation (of about 82 – 94%) in richness and diversity between plants and insects. Moreover, Tscharntke and Greiler (1995) also documented that the species richness values of several insects such beetles, bugs, bees, butterflies and moths are known to be positively correlated to the floral species richness. Therefore, as the plants increase in richness so does the insects - which make the plants a primary predictor of insect assemblages within the landscape.

Immediately after the fire many insect assemblages decline markedly depending on their agility and the degree of exposure to the flames, however, the decline is never a 100% (Swengel 2001). Following the burn some insect taxa persist in lower numbers, others may reach the normal population whereas others such as ground beetles (Coleoptera) and grasshoppers (Orthoptera) become more abundant (Nagel 1973; Anderson *et al.* 1989; Tscharntke and Greiler 1995). The decline can however, be lessened by conducting a cool early dry season burn on a small patch allowing the insects to escape to the adjacent unburnt areas. Moreover, among the negatively affected insect populations, Panzer (2002) found that about 68% recovered within a year whereas the rest of the 163 populations reached their full recovery in less than 2 years. Besides, some invertebrates such as spiders by winter would already been burrowing beneath the soil surface making then less threatened by the winter burn (Swengel 2001; Panzer 2002). This also indicates that implementing small rotational cool season burns within the landscape for promoting heterogeneity does not impose severe consequences to the insect taxa. Another importance of the structural heterogeneity as a result of patchy burning is that, not only ungulates benefit from the green flush, but also some insect herbivores are attracted too (Swengel 2001). Some invertebrates prefer short grass and bareground resulting from heavy grazing whereas others such as Hemipterans and Lepidopterans prefer tall grass or patches with many years since the last fire (Swengel 2001; Poyry *et al.* 2006). Therefore, this indicates that coupling fire with grazing as an ecological process in rangelands to promote patchiness or heterogeneity has further important implications on conservational measures in terms of creating different niches for different insect species within the landscape.

The structural heterogeneity across the grassland also has some effects on the birds' community either directly or indirectly. Habitat selection in birds is primarily determined by food supply, shelter from predators and the availability of nesting sites (Isacch and Cardoni 2011). The coexistence of different bird guilds such as insectivores in grasslands depends largely on the distribution and the diversity of insects as their food source (Little *et al.* 2013). Therefore, as with the insect community, within the avian community there are also short grass specialists, the intermediates and tall grass specialists depending on the distribution of their food source (Fuhlendorf *et al.* 2006; Little *et al.* 2013). Isacch and Cardoni (2011) recorded an almost equal number of avian species but very different in composition in short grass (28 bird species) vs. a tall grass (27 bird species) in Argentinian grasslands, which drove them to proposing a system of heterogeneous grazing as a way to promote productivity and conservation of grassland birds. For example, in short grassland they found large populations of short-grass specialists such as the Buff-breasted Sandpiper and in tall grassland, the Bay-capped Wren-Spinetail (Isacch and Cardoni 2011). Moreover, Fuhlendorf *et al.* (2006) found that greater spatial heterogeneity in vegetation as a result of fire and grazing resulted in increased variability in the grassland avian community. An increase in patchiness certainly increased the diversity of biological assemblages, and the Upland Sand piper was one of avian species found abundant within the burnt patches (Fuhlendorf *et al.* 2006). In the South African context, Little *et al.* (2013) found other species such as the Yellow-breasted Pipit to be very sensitive to any form of disturbance, whereas Kopij (2001) found one of the critical species such as the Southern Bald Ibis preferring to forage on a range of invertebrates (mostly dung beetles) in short burnt grasslands. Moreover, according to Little *et al.* (2013) in most of the annually burnt highland (high rainfall) grasslands Orthopterans are the largest in biomass (78%) among other arthropods, which supports the abundance of insectivorous birds in burnt patches.

Therefore, after taking into considering the above mentioned less severe effects of heterogeneity (as a result of fire and grazing) on other grassland factors such as invertebrates and birds community, this study focused on the combined effect of fire and grazing on grassland structure and patch attractiveness (in terms of being maintained short and palatable by grazers after fire). Even though the effect of fire on different factors in grasslands has been largely documented, however, there is still a gap in understanding the combined effect of fire and grazing on grass structure and attractiveness. It is mentioned above that Highveld (Sourveld) grasslands are characterized by high rainfall and low grazing intensity (due to low grass palatability) compared to Lowveld grasslands. However, It is also largely documented that as long as the grass is kept short it remains palatable due to short-grass swards having a high leaf to stem ratio which makes them more attractive to grazers than tall-grass swards because the leaf material has high N:C ratio (Hempson *et al.* 2014).

In the case of this study, the studied Highveld grassland is also characterised by these features of high rainfall (when compared to the lowveld grasslands), nutrient poor soils (due to soils being derived from granitic geologies and a significant level of leaching) as a result having a pretty homogenous grass sward dominated by tall unpalatable tussock grasses which are high in C:N ratios – Sourveld so the N content in the dry season is way below what grazers need to sustain themselves. The grazer densities are at an intermediate level of 21.79kg/ha but very much below rangeland carrying capacity for this ecosystem (see: Archibald *et al.* 2008; Hempson *et al.* 2014) to be able to keep the grass at short and palatable heights. So, in the normal situation grazing is not creating much heterogeneity in this grassland – perhaps partly because the large fires every 2-3 years are dispersing grazers and reducing heterogeneity. Therefore, we ask; can the impacts of small fires or discontinuous burning on grassland structure and consequent attractiveness to herbivores be used to concentrate grazing? If so, how long are these impacts likely to last, a few weeks or months (in which case, not really likely to alter species composition) or a full growing season (in which case potentially a management tool for creating heterogeneity)? Is the grass productivity high enough to overcome the grazer offtake and allow grass to grow back, or can the concentrated grazing create a positive feedback and maintain short-grass through the growing season? Usually productivity is above grazer offtake but small fires can boost grazer offtake above productivity, but for how long depends on how long that attractiveness continues (Wilsey 1996). This coupling of small fires with grazing to maintain the attractive green flush (following the burn) at short heights for a full year or growing season has not been documented in the Highveld grassland. This study therefore attempted to investigate this phenomenon.

2.2 Aim

The aim of this study is to investigate the impact of a small fire on grazer movements and grass community structure in a tall Sourveld or Highveld grassland.

2.3 Objectives

1) To assess how effective a single small fire is at attracting and concentrating grazers in a Sourveld grassland.

2) To determine how long this concentrating effect lasts (how long can grazing animals keep the grass short on the burn and how much biomass are they consuming).

2.4 Hypotheses and expectations

1) Grazing pressure will be more concentrated on the recently burnt patch relative to the adjacent unburnt patches immediately after the fire, and for the rest of the growing season due to the contrast between the quality of the green flush and the surrounding grassland. Short grass specialists will prefer shorter grass heights and will respond more strongly to this treatment than tall grass specialists or browsers (Objective 1).

2) We also expect high grass productivity or growth rate once the rains come but the concentrating effect of fire is enough to keep grass short. i.e. by the end of the growing season, only the small fire plus grazing treatment will have maintained a short grass sward (fire alone and grazing alone do not create short-grass areas). (Objective 1 and 2).

2.5 Materials and Methods

2.5.1 The study site

An experimental burn was applied in an area of about 5 hectares on the 13th June 2015 within the Kromdraai Nature Reserve (described on Chapter 1). The aim was to apply a small burn which would concentrate the grazers on the post-burn growth, and previous work in the Kruger National Park (Donaldson *et al* in press) indicated that 5ha was an appropriate size (since study had similar herbivore assemblage as this one but higher nutrient forage). All other fires on the property were suppressed in that year, apart from a few essential firebreaks on the property borders – so our experimental fire represented almost all the post-burn landscape in the reserve that year. We chose to burn in June to monitor herbivore usage during the dry season and the subsequent wet season in the Highveld there is usually sufficient soil moisture for grass to flush after a burn (O'Connor *et al.* 2004), but continued growth requires rainfall which generally only arrives in November. Therefore, the rainfall being one of the important factors that could have affected the experiment, monthly rainfall was recorded for the entire period of the study. This experiment was part of collaboration with the visual artist (Hannelie Coetzee), who transformed the burnt area into an artwork. The 5ha was burnt in the image of a small child reaching out to touch the head of an Eland (Figure 2.1). The image was plotted by a team of surveyors (Kirchoff Professional Surveyors), after which a Working on Fire (WoF) (http://www.workingonfire.org) team burned the outline in a 1m strip around the image. The final burn was also applied by WoF and was attended by an audience of interested public and art lovers who watched from the opposite hillside. This collaboration raised awareness of the management and science questions that we were addressing, and was highlighted in several publications and news articles after the event (a short film of the burn can be accessed on YouTube (https://youtu.be/quUOox1YXJA).

The fire took place at approximately 4pm in the afternoon during mild weather conditions (wind speed – 24 km/h, temperature = 23°C relative humidity = 34%) and the fuel was almost 100% cured. This produced a clean burn of intermediate intensity which removed almost all above-ground biomass at the site.

Figure 2.1: A ~5 ha patch burnt within the Kromdraai Nature Reserve plotted with 1500 GPS points by Kirchoff Professional Surveyors in the form of an image named “Eland & Benko” artwork.

2.6 Experimental Procedure

Across the 5ha burnt image (Figure 2.1), three parallel transects were set along contour lines and marked out with metal droppers. These transects extended beyond the burnt area by 20m on each side to represent control (unburnt) conditions. The same set of data was recorded every 4m along all three transects of about 200m each.

Just after the fire exclosures measuring 1m x 1m x 1m in volume were set up to represent a “no grazing” treatment. Twelve exclosures were placed in total, six on the burn and six off the burn (with four exclosures being associated with each transect). The final experimental design therefore included four treatments: fire + grazing (the experimental burn) fire + no-grazing (the exclosures on the experimental burn) no-fire + grazing (the surrounding unburned matrix) no-fire + no-grazing (the exclosures on the surrounding unburned matrix). The apertures on the exclosures were 10cm wide to prevent small-headed herbivores such as impalas from grazing inside the exclosures. Metal droppers and pegs were used to hold the exclosures in position and firmly on the ground to avoid animals moving the exclosures around.

2.6.1 Herbivore presence on the recently burnt patch

Herbivore presence at the site was monitored using dung counts and camera traps in order to quantify the utilisation of the recently burnt patch relative to the unburnt control.

2.6.1.1 Using dung counts

The dung method has been widely used in assessing animal movements in rangeland ecological studies (O'Connor *et al.* 2004; Archibald *et al.* 2005; Sensenig *et al.* 2010) and is a crude, but robust measure of herbivore presence at a site for most herbivores, except white rhino which dung in middens (Tatman e*t al.* 2000). There are problems with using dung to measure temporal patterns of herbivore usage because the decomposition rates of dung vary widely at different times of year depending on rainfall and dung beetle activity. Likewise, it is not possible to compare usage between different herbivore species. However, it is possible to use dung to test for individual species preference for different sites (for example by comparing the amount of dung found on and off our burn treatment). All dung piles (henceforth used interchangeably with "dung counts") within 2m of each transect were identified to species and counted. I also recorded whether or not the dung was found on the burnt or the unburnt site. After counting these dung piles were removed to avoid double counting. The first dung count where there was a full season of dung accumulated was excluded from the analysis. To minimise the bias of using the dung method, camera traps were also used to monitor animal movements.

2.6.1.2 Using camera-traps

To complement the dung methodology in monitoring herbivore presence, camera-traps were used. Camera trapping has been widely used in many wildlife studies such as identifying animal species occupying a certain area, monitoring absolute and relative abundance of species and habitat selection (Yasuda 2004; Bowkett *et al.* 2007; Lyra-jorge *et al.* 2008). Compared to other methods such as direct sighting, dung counts and following foot-prints, the use of camera traps is commended for various reasons. It is less costly regarding costs associated with doing fieldwork and does not require spending more time in the field (Bowkett *et al.* 2007; Lyra-jorge *et al.* 2008). The camera traps with good batteries and larger memory space can be set and left in the field for several weeks to months without having to keep driving to the site to check on them. Moreover, camera trapping is very good for monitoring shy and elusive animals and it provides precise and easier species identification as well as a better representation of crepuscular and nocturnal species (Bowkett *et al.* 2007; Lyra-jorge *et al.* 2008; Foster and Harmsen 2012). In scenarios where a single genus of mammals is having similar dung and footprints, camera trapping can also be helpful for distinguishing between them (Lyra-jorge *et al.* 2008). Therefore, this and other reasons make camera trapping one of the preferred method by many ecologists even though it also has its own methodological caveats.

One of the difficulties that many ecologists have struggled with in interpreting the camera trapping results is dealing with self-dependence whereby the data consists of a series of multiple photographs of the same species (O'Brien *et al.* 2003; Yasuda 2004; Bowkett *et al.* 2007; Abi-Said and Amr 2012). This imposes a challenge especially when wanting to count the number of individual species present at a site at a particular day. Also, camera traps when used in the traditional way only pick up the animals which are very close to the camera.

From acquiring so much knowledge from the previous studies about camera trapping I went on to implementing it in my study. My study was simply interested in in seeing whether herbivores were mostly attracted to the burnt patch relative to the adjacent unburnt matrix and for how long does this attraction persist. I therefore chose to set up the cameras in a slightly different configuration – as my intention was to contrast herbivore usage of two different areas I needed comparable measures of the presence of animals at both sites over time, and I set all the cameras to take repeated photographs (every 15 minutes from 05h00 till 20h00 every day) to have a full assessment of herbivore usage on each treatment over time.

I used 4 weather proofed camera traps (Bushnell Nature View Camera Trap HD), powered by 8 AA Lithium (each) batteries which lasted for 6 months. The Bushnell Cameras produced high quality 12mp images with full-colour resolution and an automatic day/night sensors, besides having in-built infrared-motion sensors, flash, a time-lapse (1 to 30 minute intervals, day/night or 24hour) and data packs that stamps each picture with the time and date of the event as well as the temperature recording. The sensitivity on the cameras was set to low, to avoid cameras capturing motion triggered photographs since I was only interested in time triggered photographs i.e. herbivores captured within the set 15 minute intervals daily. At the site, the cameras were set up three months before the burn to collect pre-fire animal activity data. They were installed at different camera stations around the 5ha burnt patch at a height of about 1.6m above the ground and distanced at about 100 – 200m from each other to avoid overlapping the field of view (FOV) and counting animals twice. From each camera station, each camera simultaneously viewed a section of the burn and that of the adjacent unburnt matrix and they were mounted tightly to the available tree to avoid moving and facing a different direction. Moreover, mounting them on trees was to hide them from being stolen. The area of burnt and unburned landscape inside the field of view of each camera was quantified by pacing out the distance on the ground. By setting the cameras to take pictures in 15 minutes intervals and recording the field of view, I was able to get a quantifiable measure of herbivore presence per unit area per unit time (kg/ km^2/ 15min interval daily) for each treatment for four different cameras.

2.6.2 Grass height and biomass

Before the fire, and at monthly intervals after the fire, I collected data on grass height, biomass and species composition. Every 4m along each transect I measured grass leaf table height using a tape measure and grass biomass using a disc pasture meter (DPM) (Bransby and Tainton 1977). Leaf table height was estimated as the height which included ~80% of the grass leaf material as seen in O’Reagain and Mentis (1989). This was considered a more realistic measure than maximum culm height of the sward height as perceived by a grazing herbivore (Vesey-Fitzgerald 1969; Zambatis *et al.* 2006). As described by Bransby and Tainton (1977) the DPM is now widely used when measuring the biomass (kg/ha) of the herbaceous layer through fitting a linear regression between the dry matter (DM) yield and the DPM height measurements (cm) of the standing forage (Bransby and Tainton 1977; Trollope 1983; Trollope and Tainton 1986; Stuart-Hill and Tainton 1989; Zambatis *et al.* 2006; Waldram *et al.* 2008; Booth *et al.* 2014). For this study, the biomass (kg/ha) in each transect was obtained by converting the mean DPM grass heights (cm) to biomass (kg/ha) using the calibration equation developed by Trollope (1983), $y = 340 + 388.3x$, where; y = estimated standing grass crop (kg/ha) and x = mean disc height (cm). This calibration was performed in the Lowveld but on similar tussock grasslands, so is likely to be an adequate estimation of the biomass and fuel loads.

Once a year (at the beginning of the study) I also identified about 5 dominant grass and forb species under the area of a DPM. The unknown grass and forb species were collected and immediately pressed for further identification in the herbarium. Similar grass height and biomass data were taken monthly inside the exclosures – four records at each corner and one in the centre of the exclosure.

The monthly data collection on the transects continued from June 2015 until June 2016 resulting in 12 months of data. Unfortunately data collection on the exclosures only started in October 2015 resulting in 9 months of exclosure data.

2.7 Data Analysis

The R program (version 3.4.0) was used for all data analysis in this section. In addition, pivot tables in Microsoft Excel as well as the Graph Pad Prism program (version 7.02) were also used to construct graphs and other analysis detailed below.

2.7.1 Herbivore presence on the burn

2.7.1.1 Dung counts analysis

In R, a Chi-squared (χ^2) test was used to analyse dung distribution of the five most dominant herbivore species at the site across 6 different grass table height classes.

A comma delimited (CSV) file from Microsoft Excel containing data on dung counts from different grazer species and grass table height along all three transects was imported into R for dung analysis. The data from the three parallel transects were pooled together for this analysis since I was only interested in dung counts at different grass heights. Since the grass table height was a continuous variable across different transects and for the duration of the sampling period, I therefore, decided to categorise it into different “height classes”. To determine the size of the classes I firstly plotted the dung counts recorded during the entire period of the study for all herbivore species against the grass table height. I then categorized the grass table height into 6 height classes (0-10, 10-20, 20-30, 30-40, 40-50 and 50-150). Shorter grass heights were to be associated with the burnt area since the surrounding grass was to stay taller during pre and post-fire.

Then, I categorized the *observed* dung counts according to the created height classes for each species in all three transects and calculated the total dung counts for all the dung in each category, which I referred to as the *available* dung. For the chi squared test, the "Expected" dung counts for each species was calculated using the equation: Expected = $\frac{Observed \text{ x } Available}{\sum Available}$, where; the *observed* was the total dung counts per each species in each height class, the *available* was the *observed* dung counts of all species combined in each height class and the sum of *available* was the total *observed* dung counts across all species and across all height classes. The Chi squared test was then calculated for each herbivore species as the sum of Observed minus expected dung counts squared over the expected dung counts (per species) using the formula: $\chi^2 = \sum \frac{(Observed - Expected)^2}{Expected}$, to get the χ^2 statistic. The degrees of freedom were then calculated as (no. of rows – 1) x (no. of columns – 1), i.e. (6-1)*(2-1) because the number of rows was the no. of height classes and the number of columns was the height class column and the observed dung counts column. After calculating the χ^2 statistic and the degrees of freedom I then used the χ^2 table to compare the calculated χ^2 statistic to the χ^2 table under the calculated degrees of freedom. Where the χ^2 statistic was higher than the χ^2 table, I rejected the null hypothesis that there was no significant difference between the expected and the observed dung counts per each herbivore species.

I further calculated the proportions (0-1) of the observed and the expected dung counts per each height class for each grazer species as $\frac{Observed}{\sum Observed}$ and $\frac{Expected}{\sum Expected}$, respectively. This was used to plot graphs of observed minus expected dung counts at different height classes to see at which grass height were the herbivores mostly observed than expected. Again, the monthly data was pulled together as the case with the three transects.

2.7.1.2 Camera-trap data analysis

Since the camera data did not follow a normal distribution, a nonparametric Wilcoxon sum rank test was used in R to compare herbivore distribution between the burnt and the unburnt matrix during the course of the study period.

All the 15minute daily recordings of herbivore presence either on the burn or off the burn were recorded on an Excel spreadsheet for the entire period of the study according to herbivore species. On the excel spreadsheet the herbivore biomass (kg/km^2) was calculated by multiplying the mass of each recorded herbivore species taken from literature (Table 1.2 in Ch. 1) by the area of the FOV where each camera was facing (either on the burn or off the burn). This was done because each camera viewed a different proportion of burnt and unburnt vegetation, so the counts on the burnt/ or unburnt vegetation needed to be converted into a metric that was comparable between treatments. For instance, there were times where the cameras stopped working due to different technicalities; those missing dates were taken note off by having another column in excel indicating whether the camera was working or not in all 15minute daily intervals.

In R, the monthly data were arranged sequentially for the entire period of the study using the “strptime” and “strftime” functions. I then looked at preference for the burnt landscape over time by comparing the density of herbivores on and off the burn each month with a Wilcoxon sum rank test. I used this non-parametric test because the data were zero-inflated (many zero values). For this analysis I used the individual 15 minute values and pooled all the data from all four cameras in each month.

Using the Pivot tables in Excel, I calculated the mean (μ) herbivore biomass (kg/km^2) and the standard error of the mean (*SEM*) for each month and for each treatment (burnt and unburnt) in all four cameras combined (μ kg/km^2 & *SEM* per month per 4 cameras combined). I chose to calculate and include *SEM* in my graphing because it is one of the important statistical measures of variability around the means – as the sample size increases the standard error decreases due to less dispersion around the population mean (Barde and Barde 2012). Therefore, the *SEM* herbivore biomass for each treatment was obtained by dividing the standard deviation (*SD*) by the square root of the number of records (*n*) for each month, ($SEM = SD/\sqrt{n}$ per each month). I then imported the monthly means, standard errors, and total number of records into the Graph Pad Prism program (version 7.02). Using the Graph Pad Prism program I plotted the monthly means plus standard errors for the two treatments to see which treatment recorded the highest monthly herbivore biomass density during the entire sampling period. Since the calculated monthly statistical parameters (means and standard errors) were from the daily 15min data and all cameras combined, therefore, cameras and the daily 15minute recordings were treated as pooled data.

To see which grazer species preferred the burn at different months of the sampling period, a grazer preference index or a selectivity index was calculated using Excel pivot tables for each of the most common grazer species and graphed using a Graph Pad Prism program (version 7.02). This was to help me tell whether the species that were attracted after the fire were the same as the species which were attracted throughout the rest of the growing season. Therefore, using pivot tables I grouped all four cameras together as replicates because analysing each camera did not show any clear pattern due to insufficient data as cameras were faulty at some points. Therefore, due to this inconsistence in operational times of some of the cameras, I had to calculate the number of trap days for each month rather than assuming that the number of trap days was equal to the monthly calendar days. This calculation was done as: *no. trap days per month* = *total counts of photographs per month* (in all cameras) ÷ [*total daily hours set on a camera* x *four 15min intervals* (to make an hour) x *2 treatments* (since cameras were simultaneous facing both treatments) x *4 cameras* (all cameras grouped together)]. Therefore, the number of trap days never exceeded the number of calendar days for each particular monthly, instead they were lower or equal (depending on whether the cameras were fully operational for that month). I then calculated the monthly total number of grazers (per km^2) per species in each treatment as: *species abundance* per month = *sum of that species per* km^2 per month ÷ *no. trap days* per month, in both treatments. Finally, I calculated the preference for the burn index for each grazer species as: *species abundance* per month on the Burnt ÷ (*species abundance* per month on the burn + *species abundance* per month on the Unburnt). The preference index therefore was to range from 0 – 1, where 0 equals complete avoidance of the burn and 1 indicates complete preference for the burn (Sensenig *et al.* 2010). I then used a line graph in Graph Pad Prism to plot those monthly preference scores for each grazer species.

2.7.2 Grass height and biomass analysis

In excel, both grass table height (cm) and the converted grass biomass (from cm to kg/ha) were entered accordingly for the four fully factorial treatments, a) fire + grazing (exposed burnt), b) fire + no grazing (exclosed burn), c) no fire + grazing (exposed unburnt patch and d) no fire + no grazing (exclosed unburnt patch). From the original spreadsheet cleaned of data errors, I used the pivot tables to calculate the averages (*mean*), standard deviations (*SD*) and the total number of records (*n*) per each month for both grass table height and grass biomass on all four fire treatments. These calculations done on *n* records per each month were done by grouping all three parallel transects together as replicates. The monthly *n* and *SD* were again used to calculate the monthly standard error of the mean (*SEM*) as $SEM = SD/\sqrt{n}$. I then imported the data (monthly *mean*, *SEM* and *n*) for both grass table height and biomass into Graph Pad Prism (version 7.02) to plot the graphs for both variables according to the fire treatments. In addition I also imported the rainfall data into the same file in Graph Pad Prism and plotted the recorded monthly rainfall alongside grass table height and biomass (using a "combine graphs" feature within the program) to see how the results related to the monthly rainfall.

In R (version 3.4.0) prior to the analysis, I checked for normality of the grass table height and biomass data by plotting histograms and checking for the skew-ness of the data. Realising that the data followed a normal distribution, I proceeded to use a Paired T-test to compare grass height and biomass between the grazed burnt patch (Burnt) and the ungrazed burnt patch (Burnt + Exclosure) for the Month of October 2015. This was done to see if there was already any difference in grass height and biomass between the exclosures and the exposed plots one month after installing the exclosures. Even though there was low rainfall at the time, however, a difference in biomass and height was to show an indication that the grazers are actually grazing on the patch and keeping the grass short. I further used a T-test between the grazed burnt patch and the ungrazed burnt patch for the entire period of the study after the fire treatment to see if the grazers managed to keep the grass short for the duration of the study. In R, this t-test was run on all post-fire months grouped together and treating the three plots as pooled data.

A One-way Analysis of variance (ANOVA) was done to see whether the grass managed to regrow to the previous year's height and biomass. For this, I compared the Unburnt March 2015 data to the March 2016 data of all four variables (Unburnt, Unburnt + Exclosures, Burnt, Burnt + Exclosure). Significant differences at $p < 0.05$ were further tested using Tukey's HSD multiple comparisons' post-hoc test. A no significant difference (expected on the other three variables besides the Burnt treatment) was to indicate that the grass had regrown to its original size. Moreover, ANOVA was also used to compare both grass height and biomass among all four treatments for the entire period of the study after the fire implementation – therefore, grouping all months postfire as repeated measures and the three plots/ transects as replicates. I also repeated this ANOVA analysis for the month of June 2016 (last month of the sampling period) to see the differences among the treatments in grass height and biomass at the end of the experiment, pulling data from all three transects together.

2.8 Results

When I started sampling in March 2015 the monthly rainfall values were around 60mm, they continued to decrease to almost nothing in June when we implemented the experimental fire, until it picked up again to just 80mm in September 2015 (Figure 2.2). These early rains did not continue, however, and the site experienced below-average rainfall for October to December 2015, (Figure 2.2). When comparing the sampling year 2015 to other previous years, I can safely say 2015 was a drought year as it received an annual rainfall of only 450mm compared to the previous 3 years which all received above 600mm of rainfall each (Figure 1.2). Despite this, there were several months of good rain from January to March (Figure 2.2).

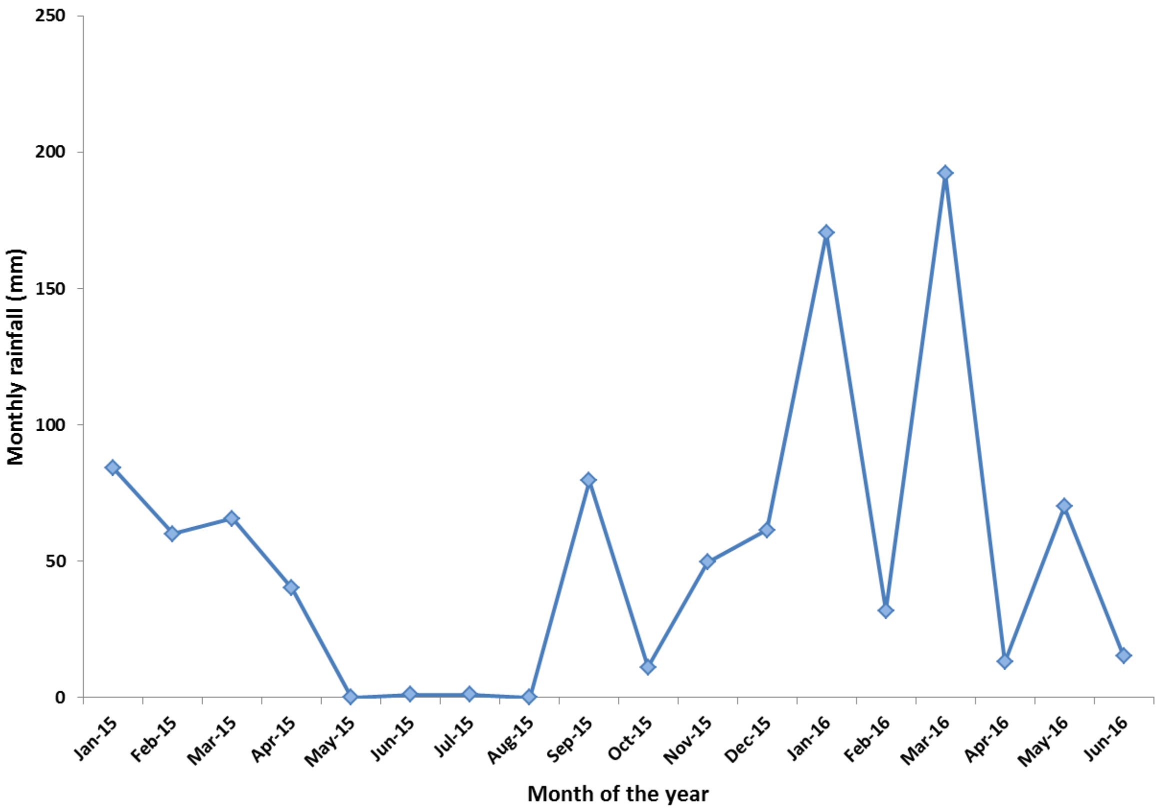

Figure 2.2: Monthly rainfall for the sampling years 2015 – 2016. The sampling started in March 2015 and ended in June 2016, making a total of 16 sampling months.

2.8.1 Herbivore presence on the recently burnt 5ha patch

Results obtained from the dung counts (n =2744) indicating herbivore preference in relation to different grass height classes, and from the camera data comparing grazer biomass between the burnt and the unburnt treatments.

2.8.1.1 Herbivore preference for different grass heights

Herbivore preference for different grass heights at my site followed what would be expected from the literature. The Blue wildebeest showed a preference for shorter grass: their preference to be found foraging or grazing on shorter grass height of below 10cm was much higher than expected (Figure 2.3a). Any height class exceeding 10cm was avoided by the wildebeest, especially the height class of 21- 30cm (Figure 2.3a). The blesbok and the red hartebeest also preferred foraging on shorter grass height of less than 10cm, but this was significantly different from expected for blesbok and not significant for red hartebeest (Table

2.1). (Figure 2.3b,c). They also avoided foraging at any grass height taller than the 10cm threshold, with the least preference for the grass height class of 21-30cm (Figure 2.3b, c).

In contrast, impala showed no particular preference for any grass height class (Chi-squared test not significant in Table 2.1) and zebra strongly avoided the shorter grass heights (they were observed on the 0-10 height class less than would be expected based on its availability). The impala, mostly preferred to forage on grass within the height category of 11-20cm, and less within the 31-40cm category, and any grass height above these two categories was avoided (Figure 2.3d). The zebra, on the other hand showed a clear affinity for foraging on taller grass in the 11-20cm and the 21-30cm category (Figure 2.3e). Above 30cm grass height the preferences by the zebra was not clear (Figure 2.3d)

Table 2.1: The Chi-squared (χ^2) results of grazer-dung counts found at the study site. The analysis compared dung counts across grass height classes – testing the expectation that there should be equal numbers of dung in all classes. The calculations were done manually in "R" using the formula $\chi^2 = \Sigma [(O_i - E_i)^2)/E_i]$, where O_i represents the observed and E_i the expected dung counts within each of the six categories. Any calculated χ^2 values greater than the χ^2 table values indicated a significant difference and vice-versa.

Grazer spp.	**χ^2 statistics**	**χ^2 table**	**D.f**	***p* – value**
Wildebeest	16.44	15.086	5	0.010
Blesbok	19.05	16.750	5	0.005
Red hartebeest	7.96	11.070	5	0.900
Impala	2.81	11.070	5	0.900
Zebra	59.77	16.750	5	0.005

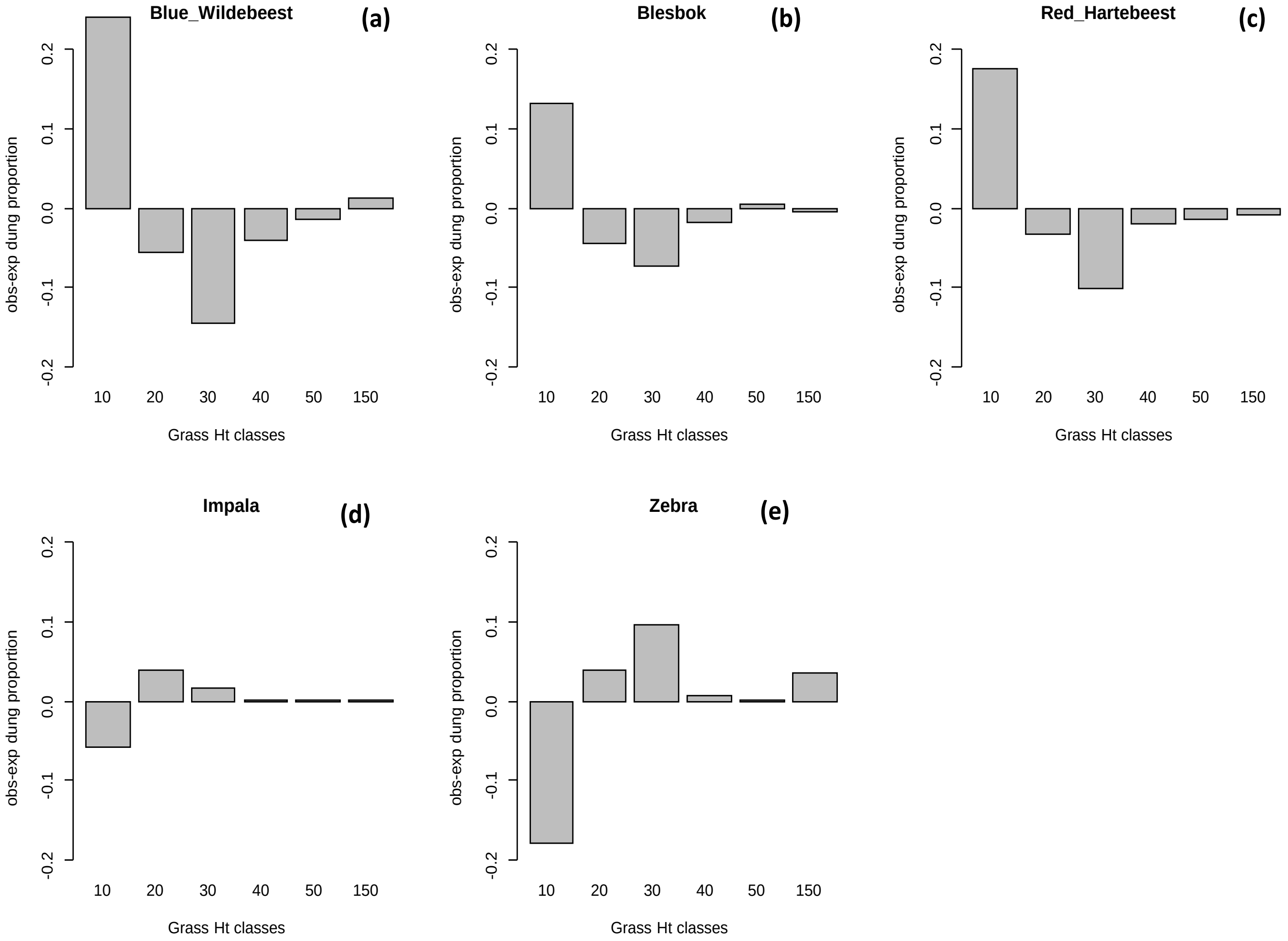

Figure 2.3: Observed minus Expected (O-E) dung proportions relative to increase in grass table height (cm) categorised in height classes (0-10, 11-20, 21-30, 31-40, 41-50, 51-150 cm).

2.8.1.2 Using camera-traps

The camera trap data showed clearly that after the burn in June 2015 most herbivores spent significantly more time (Wilcoxon signed rank test: $p< 0.05$, $N = 79300$) on the Burnt patch relative to the adjacent unburnt matrix for most of the months soon after the fire (August, September October 2015) and after the late January 2016 rainfall (January, February, April and May 2016) (Figure 2.4). Before the 5ha burn the herbivores were randomly distributed across the landscape with no significant difference (W = 21720591, $p = 0.304$, n = 20557) from March – June 2015) between the area of the burn and the area around it within each month. However, after the burn (June 2015), they started to increase in numbers on the burnt patch (Figure 2.4). The herbivore biomass then consistently became higher on the 5ha patch after the burn compared to the unburnt matrix every month until the end of the experiment (June 2016) (Figure 2.4) even though the difference was not significant (Wilcoxon signed rank test: $p > 0.05$) in other months (July, November, December 2015, and March and June 2016).

When comparing the average herbivore biomass density between the burnt and the unburnt matrix (for each month on all four camera data pooled) I found that in the month of July 2015 (few weeks after the fire) there was still no significant difference (W = 16097296, $p = 0.81$, n = 5673) between the two treatments. However, in the followed August, September and October 2015 the difference was highly significant (W = 16662307, $p < 0.05$, n = 5673, W = 13247507, $p < 0.05$, n = 5003 and W = 28940322, $p < 0.05$, n = 7564, respectively. Moving on to November and December 2015 the difference was not significant (W = 3606016, $p = 0.61$, 2684 and W = 6714101, $p = 0.35$, 3782, respectively). The difference then became highly significant on the following January and February 2016 (W = 14762133, $p < 0.05$, n = 5490 and W = 10188992, $p < 0.05$, n = 4941, respectively). In March and June 2016 the difference was not significant (W = 7306678, $p = 0.06$, n = 3965 and W = 7927615, $p = 0.73$, n = 3660, respectively) but it was significant for March and May 2016 (W = 6989761, $p = < 0.05$, n = 3965 and W = 13031746, $p < 0.05$, n = 5002). When relating the herbivore distribution (between the burnt and the unburnt matrix) to rainfall, the rainfall had an indirect positive effect on the on herbivore distribution by directly affecting the growth rate of the grass on the burn (as seen on the following Section 2.8.3). The months where there was no significant difference in herbivore distribution are the same months where there was no or very little rainfall (Figure 2.4 and 2.2).

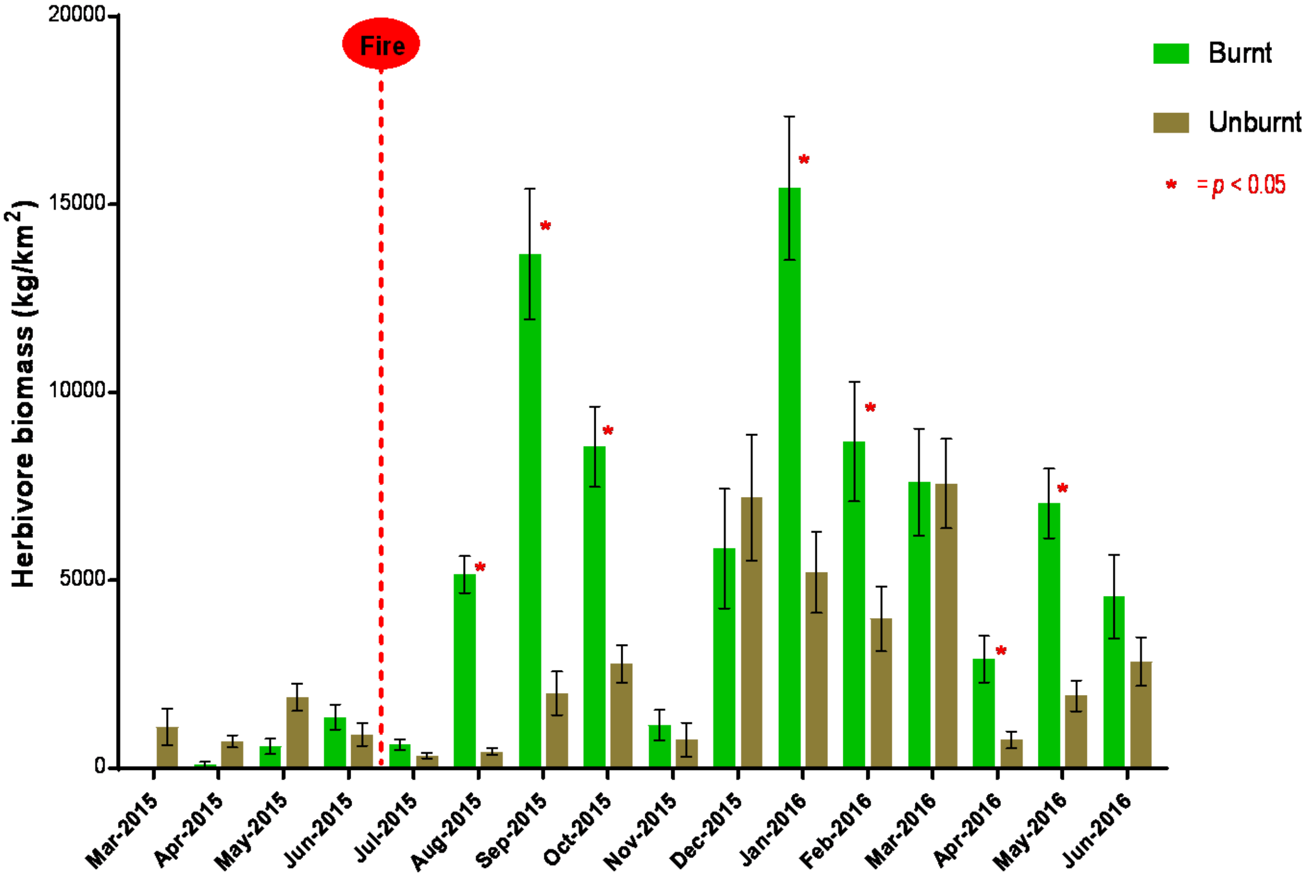

Figure 2.4: Average monthly (averaged from the 15minute time steps from all cameras pooled) herbivore biomass (kg/km^2) or presence inside the 5ha experimental burn relative to the surrounding unburnt matrix recorded in 15minute intervals daily (05h00 – 18h00) from March 2015 to June 2016 (15months). Plotted are means and standard errors of the means (mean ±SE). The red dotted line indicates the month (mid June 2015) when fire was implemented and the red stars indicate the significance difference within each month between the burnt and the unburnt matrix.

As with the monthly herbivore biomass presented above, the grazer preference index seemed to show a similar pattern by not showing any clear preference by grazers for any of the two patches before the fire. However, after the fire most grazers moved into the burn and stayed there most of the time during the sampling period. For instance, the impala, which showed no clear pattern previous (Section 2.8.1.1) when comparing dung counts against grass height now showed a very conspicuous trend by consistently staying on the burnt patch all the sampling months post-fire with a preference index ranging between 0.8 – 1 (Figure 2.5). The blesbok also stayed on the burn (preference index above 0.5 throughout post-fire) during all the sampling months post fire (Figure 2.5). Moreover, wildebeest also showed more preference for the burn during most of the post-fire sampling months (August, September, October and November 2015) (Figure 2.5). The months when blesbok and wildebeest preference scores dropped were months with very little rain (Figure 2.2). The zebra as a bulk feeder seemed to forage interchangeably on- and off-the burn. They preferred the burn one month post-fire and reverted back to the unburnt tall grass and resurfaced again on the burn in October and November 2015 then went back to the tall grass in December 2015 during the drought. However, after the late rains in January and March 2016, the zebra went back to the burn and stayed there for the remained post-fire sampling months with intermediate preference scores for the burn ranging between 0.5 – 0.7 (Figure 2.5).

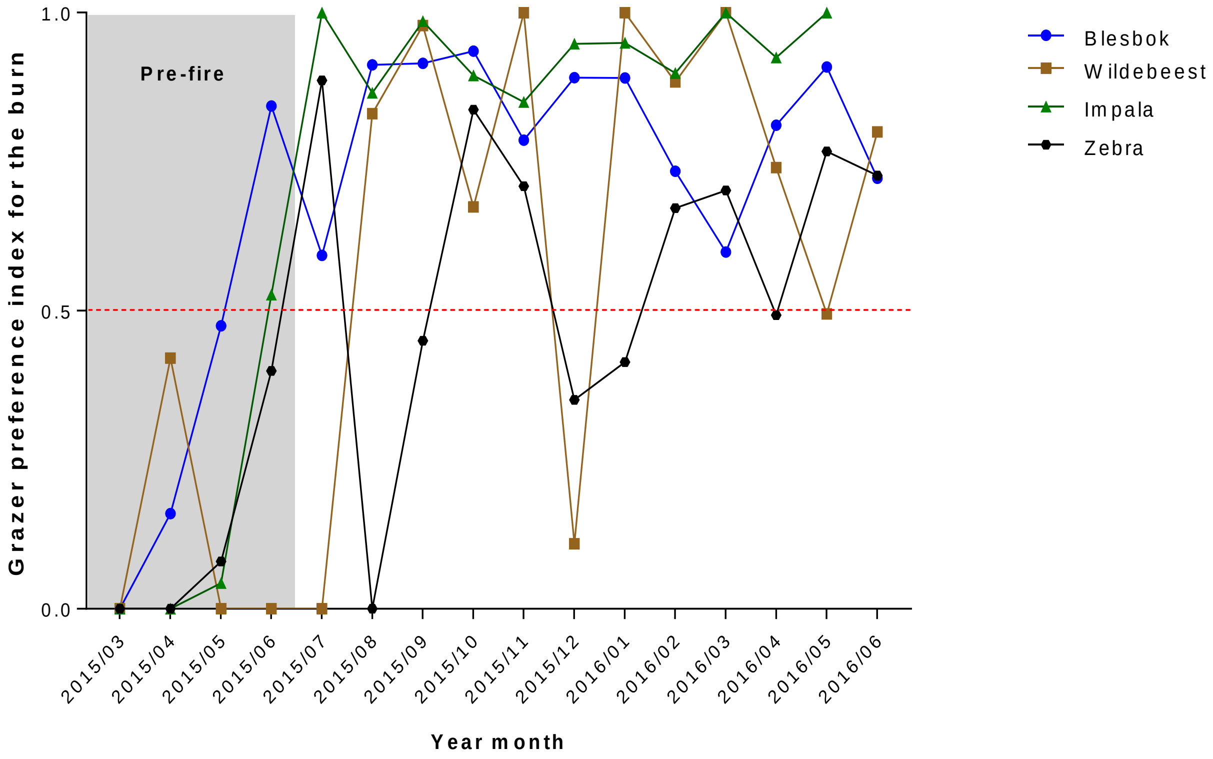

Figure 2.5: Grazer preference for the burn index plotted for each month, for each of the most common herbivore species at the site. Any preference score above 0.5 (red dotted horizontal line) indicates preference for the burn and the scores closest to 1 indicate the highest preference and vice-versa. The vertical grey block indicates the pre-fire period and thereafter, the post-fire period.

2.8.2 Grass height and biomass

Both grass table height and grass biomass yielded a similar trend of results hence I decided to present them together alongside each other in this section.

After the fire event (June 2015), the grass on the exposed burnt patch (“Burnt”) flushed within few weeks to an average height and biomass of about 6cm and 1700kg/ha, respectively (Figure 2.6). It then persisted at this lower level until the start of the rains – which were late and only arrived in January 2016 (Figure 2.6). Growth during the rainy season on the burnt and grazed plot was never sufficient to increase grass height above 10cm – the preferred grazing height for many of the grazer species (see Section 2.8.1.1), and so by the end of the growing season the burn was still an attraction for grazing animals (Figure 2.6). However, the grass on the burnt + exclosure treatment regrew to pre-fire levels by February 2016 and the exclosures recorded values slightly higher than those on the exposed unburnt treatment (Figure 2.6). Both grass height and biomass then stayed this high until May 2016 only dropping slightly (to 16cm and 3200kg/ha, respectively) in June 2016 (as it did the previous year's June), following the late high rainfall received in January and March 2016 (170ml and192ml, respectively) (Figure 2.6).

When using a t-test for the month of October 2015 I found that one month after installing the exclosures inside the burnt patch, the grass grew significantly higher in both height and biomass ($t_{83.57}$= 3.7526, $p < 0.05$ and $t_{38.11} = 3.3168$, $p < 0.05$, respectively) inside the Burnt+Exclosure treatment compared to the Burnt treatment (Figure 2.6). The difference between the two treatments (Burnt and Burnt+Exclosure) for the entire duration of the study after the fire treatment was highly significant (t-test: $t_{304.08} = 20.236$, $p = < 0.05$ and $t_{283.68} = 17.4960$, $p < 0.05$) for both grass height and biomass, respectively, such that the grass on the exposed burnt plots was consistently grazed short irrespective of the late rains which caused an exponential growth inside the exclosures (Figure 2.6).

When comparing the grass height values for the Unburnt March 2015 vs. all 4 treatments in March 2016 (following the January rainfall that year) I found that the grass managed to regrow to pre-fire height in three treatments (ANOVA: F (3, 266) =20.08, $p < 0.05$) and a post-hoc comparison using Tukey's test showed that only the Burnt treatment differed from the Unburnt March 2015 (Figure 2.6A). Using the same analysis, the grass biomass (ANOVA: F (3, 266) =58.76, $p < 0.05$) also remained the lowest inside the exposed burn and became the highest inside both exclosure treatments, however, unlike the grass height it slightly fell short to reach the pre-fire biomass values on the exposed unburnt treatment (Figure 2.6B). However, for the entire period of the study after the burn I found that there was a significant difference (ANOVA: F (3, 3339) = 158, $p < 0.05$ and ANOVA: F (3, 3339) = 258, $p < 0.05$) in both grass height and biomass respectively among these four treatments. Using the Tukey HSD post-hoc test, the differences existed between all combinations or comparisons except for Unburnt+Exclosure vs. Burnt+Exclosure in grass height – which were the highest followed by the grazed unburnt and lastly the grazed burnt patch which was up-to 60% shorter compared to the other three treatments, throughout the sampling period post-fire (Figure 2.6A). The grass biomass also followed the same pattern, except that the Burnt+ Exclosure significantly differed from the other exclosure treatment even though the exclosure treatments were the highest for the entire period of the study compared to the other two treatments (Figure 2.6B). At the end of the experiment (June 2016), the same pattern still existed for both grass height and biomass. The grass height did not significantly differ among the exclosure treatments and the exposed unburnt but all three treatments significantly differing to the grazed burnt patch (ANOVA: F (3, 266) = 36.71, $p < 0.05$, Tukey's post-hoc test), whereas the biomass significantly differed among all comparisons except for the exclosure treatments (ANOVA: F (3, 266) = 41.76, $p < 0.05$, Tukey's post-hoc test).

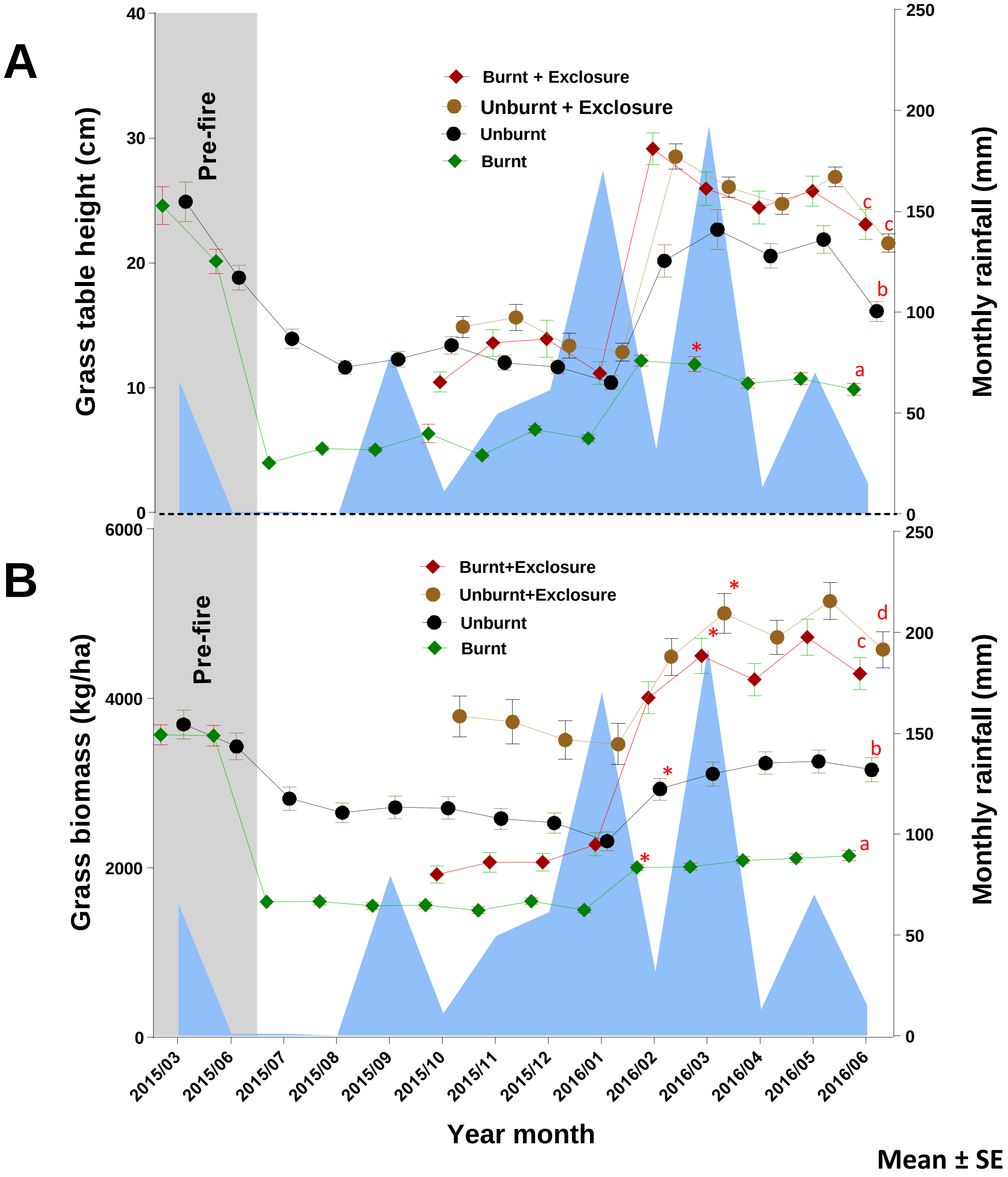

Figure 2.6: A fully factorial design for the fire treatment of average monthly grass table height (cm) and biomass (kg/ha) sampled twice (March and June 2015) during pre-fire (grey) and monthly (July 2015 – June 2016) thereof post-fire on the burnt 5ha patch. Shown is the effect on grass height and biomass of: a) fire + grazing (Burnt), b) fire + no grazing inside the exclosures (Burnt + Exclosures), c) no fire + grazing (Unburnt) and d) no fire +

no grazing on inside the exclosures (Unburnt + Exclosures). Plotted are mean±SE and the monthly rainfall (mm) in blue on the secondary y-axis. Red stars indicate significance difference in grass height and biomass for each of the four treatments in the month of March 2016 compared to the Unburnt in March 2015 and red letters indicate significance difference among all treatments for the duration of the experiment.

2.9 Discussion

These results clearly demonstrate how the interaction between fire and grazing can be an effective tool for manipulating grassland structure. Fire alone has a very ephemeral effect on grass height, and within 1-2 months (February 2016) after the rains arrived, the burnt and ungrazed treatment was statistically indistinguishable from pre-fire conditions – and the growth rate levelled slightly higher than on the exposed unburnt (Figure 2.6) indicating that even though most grazers preferred the burn with short grass however, some grazers such as zebras still stayed on the unburnt plots with taller grass (see Section 2.8.1.1). Moreover, grazing alone in these tall-grass areas is not sufficient to impact grass height or end of season productivity: the grass in the exclosure treatments showed exactly the same seasonal patterns as the grazed landscape. The grass on the exposed burnt area was consistently grazed shorter, whereas in other three treatments the grass significantly increased in height and biomass soon after the late rains. When comparing all four treatments, only the fire + grazing treatment maintained the short grass habitat for a full growing season (Figure 2.6): growth during the rainy season on the burnt and grazed plot was never sufficient to increase grass height above 10cm – the preferred grazing height for many of the grazer species (Figure 2.3), and so by the end of the growing season the burn was still an attraction for grazing animals. Therefore, how long these short-grass areas persist depends on feedbacks between short-grass grazers and grass productivity. In this case, we burnt a very small fire (5ha), which attracted high densities of grazers and it was also a low rainfall year, so the grass remained short (<10cm) all the way through the growing season.

Within few weeks after the fire in June 2015, the grass flushed out due to the residual moisture still present in the Sourveld soils (O’Connor *et al.* 2004). Personally, I think this indicates the importance of implementing early burns in sourveld grassland when the residual soil moisture is still there to promote growth before the rain season. Because the rains arrived very late – only really starting in January 2016, there was very little productivity on any of the treatments for the first half of the season. Thus, unlike in more average rainfall years, there was only about a 4 month (rather than a 6 month) period when grazer off-take needed to match grass productivity to keep the grass short, and this clearly happened (Figure 2.6). Both grass height and biomass inside the exclosures increased significantly after some very good months (January 2016 and March 2016) of rainfall resulting to a huge distinction from the growth on the grazed burnt treatment which was constantly grazed to up-to 60% shorter than the other treatments' heights. Sensenig *et al.* (2010) also found lower grass biomass on the burnt areas by about 20-60% when compared to the unburnt areas in the Laikipia District in Kenya. Noy-Meir (1995) also reported a reduced grass cover and height on the burnt area relative to the adjacent unburnt in the Mediterranean grasslands.

This fire treatment in my study was effective for two reasons; firstly the fire that was applied was very small – 5ha is not the usual size for management burns, which usually are applied to blocks of several thousand hectares. It was therefore quite an unusual example of the fire-grazer interaction because past studies have demonstrated a strong attraction of all herbivores for the post-fire regrowth but this effect usually dissipates within a few months as the burnt grassland grows back under very low grazing pressure because the animals are dispersed within the burn scar (Archibald *et al*. 2004). Therefore, to show that this type of burn had a strong effect in attracting herbivores and therefore, keeping the grass short throughout the year, is a novel result, and important for managers to consider – both as a management tool, and in terms of unintended consequences of the application of small fires (e.g. fire breaks). Moreover, I showed that this treatment is effective in maintaining short grass in sourveld areas with high productivity – although the low rain in the year of the experiment means it is still not clear how generalizable these results are.

When linking the grazer presence results from camera data to the ones on dung counts I found that there was a strong similarity in most cases. For instance, both methods presented that grazers such as blesbok, wildebeest and hartebeest have a stronger affinity for the shorter grass post-fire, whereas the zebras balance their diet by grazing interchangeably between the burn and the unburnt. These short-grass specialists (blesbok, wildebeest and hartebeest) continued to prefer the burnt site as the season wore on due to the fact that as small bodied ruminants, they require high forage quality, which is readily available in short grass whereas, the larger- bodied zebra as bulk feeder and a hindgut fermenter require high forage quantity which was mostly available outside the burn (Sensenig *et al.* 2010; Allred *et al.* 2011). The short-grass specialists represent 40% of the herbivore biomass at the Kromdraai Nature Reserve, and are common species across the Highveld (Skinner *et al.* 1974; Boshoff and Kerley 2015), so this management intervention is a potentially useful tool for increasing the area of preferred habitat for these species.

Even though the impala did not show a clear selection for shorter grass height (from dung analysis), however they also had a high preference for the burn (Figure 2.5). The reason why impalas showed no clear grass height affinity could have to do with the fact that they are mixed feeders (Du Toit and Cumming 1999). Regardless of the attractiveness of the fresh green flush, they also spent some time off the burn foraging on forbs and tree leaves. The zebra however, mostly preferred foraging off the burn where the grass was taller, and only coming to the burn few times during the rainy season (Figure 2.5), also seen in (Arsenault and Owen-Smith 2011). This was due to the fact that as opposed to small ruminants, zebras are larger herbivores and they are hindgut fermenters which makes it more reasonable for them to go for forage quantity than quality (Wilsey 1996; Augustine and Derner 2014). Sensenig *et al.* (2010) also found that hindgut fermenters had a lesser preference for the burnt patch than other foregut fermenters and that body size was inversely proportional to preference for the burnt areas in a study done in Kenya.

Putting this study in the context of other previous studies across the globe, Allred *et al.* (2011) found that ungulates preferred to forage on recently burnt areas relative to patches with long time since fire in a Tallgrass praire. Wilsey (1996) also found that the wildebeest and impala were more abundant on the burnt area relative to the unburnt area on a study done in the Serengeti National Park in Tanzania. Moreover, Archibald *et al.* (2005) also found that burnt areas drew herbivores off the neighbouring unburnt grazing patches. This magnetic effect of the burnt areas was due to the attractiveness of the short green flush which is highly palatable (Sensenig *et al.* 2010). In another study by Talbot and Talbot (1963) in the Massailand, East

Africa, focussing on wildebeest, they also found that the wildebeest mostly preferred foraging on grass height less than 10cm regardless of grass species palatability. Any grass sward higher than this threshold was avoided and it triggered the movement of the wildebeest to other grazing plains (Talbot and Talbot 1963). All these data together suggest that the grass community level palatability is more important in determining grazer movements than grass species level palatability, and that unpalatable grasses can become more palatable to many herbivores when they are short. These findings correspond with the findings of my study. Despite the fact that they found that the zebra did not show any clear preference, they also found that preference for the burnt site was negatively related to the average herbivore body mass (Wilsey 1996) as seen in Sensenig *et al.* (2010) as well as in this study. This meant that smaller bodied herbivores mostly preferred high-quality low-quantity forage on the burn (Sensenig *et al.* 2010; Allred *et al.* 2011) whereas, larger herbivores preferred low-quality high-quantity forage on the unburnt site (Sensenig *et al.* 2010; Allred *et al.* 2011), which is the same pattern observed in my study.

In other studies as well, it is also evident that the wildebeest and blesbok also play a crucial role in maintaining grass at short heights and establishing short sward grazing patches. For instance, in the Mountain Zebra National Park in the Eastern Cape Province in South Africa, Novellie and Gaylard (2013) found that the blesbok was able to establish short-statured grassland and maintain them for a period of over 20 years. In another study also done within South Africa, Yoganand and Owen-Smith (2014) found that wildebeest also established short grass grazing patches on the nutrient-rich Lowveld soils in the Orpen region of the Kruger National Park. The study in Mountain Zebra National Park is in a similar Sourveld grassland, and corroborates that these short-grass patches are an appropriate habitat-type in these ecosystems. However, in another study in a similar system by Tomor and Owen-Smith (2002) showed that in the Nylsvley Nature Reserve grazers such as wildebeest stayed on the burn for the duration of their study, unfortunately, their study period was very short (only 4 months compared to the whole 12 months in my study) and they did not measure the grass height to see whether those grazers managed to keep the grass short by consistently grazing on the burnt patch.

2.10 Conclusion

All three of my hypotheses were supported by the data collected here and the two methods for; grazer presence (dung counts and the use of camera-traps) as well as for quantifying growth (grass height and biomass) yielded similar results, therefore adding more assurance on the results found. This study showed that it is possible to use the interaction of fire and grazing to create short-grass areas in tall Highveld grasslands. Grazers managed to maintain the grass short on the burnt patch during the entire period of the study in a Highveld grassland, which is one of the major novelties of this study. Although many other studies have shown a short term response of grazers to the post-fire green flush (Tomor and Owen-Smith 2002) no other study that I know of has looked at the impacts of fire over a whole growing season. It would take more years of data, and a range of fire sizes to determine how effective this fire application is in creating and maintaining short-grass ecosystems in the Highveld, but this study shows that it is certainly possible, and that these habitats are highly preferred by many of the indigenous herbivores on the Highveld. Among other grazers at the site, the wildebeest, blesbok and the hartebeest played the most significant role in keeping the grass short on the burnt 5ha plot. This is such an important finding which could be very helpful to rangeland managers in deciding which antelopes to keep in their farm when wanting to create these short-grass grazing “hot-spots”, especially in sourveld grasslands where grasses are generally unpalatable when tall. Therefore, these results indicate that with the use of small fires and appropriate grazers, grazing “hot spots” can be created and maintained.

3 Chapter 3: LONG-TERM IMPACTS OF FIRE AND GRAZER INTERACTIONS IN A HIGHVELD GRASSLAND.

3.1 Introduction

In recent years there has been much interest in understanding interactions between fire and grazing as the two most important disturbances in grasslands. Generally it has been found that these disturbances are complementary and create a moving mosaic of burnt, then grazed, then rested patches in a landscape (Brockett *et al.* 2001; Fuhlendorf *et al.* 2009). This is due to the fact that grazers are attracted to the post-burn landscape, and come and keep the grass short, until the next fire, which moves them off to another burn patch (Allred *et al.* 2011; Archibald 2008). Fire has been used in this way in South Africa to create rotational grazing schemes without fences (Teague *et al.* 1981; O'Connor and Crow 1999). However, this same interaction could result in intensively utilised patches that persist in one place if no new burns are implemented somewhere to draw grazers off the old burn being utilised. Although this is a fairly artificial phenomenon (fires are more likely to occur on grasslands with enough fuel) it has been touted as a management intervention that can act to break up a tall-grass landscape and create short-grass patches (Chapter 2). If small discontinuous burns were to occur in the same patch of land without being rotated, then they could potentially create a grazing 'hot-spot' (Anderson *et al.* 2010; Arnold *et al.* 2014) that would not only increase structural heterogeneity but might result in a shift in species composition *(*Veen *et al.* 2008). Repeated small fires in exactly the same place in the landscape can have very different impacts from normal landscape-level fires because instead of a shifting mosaic of grazing you would be creating a situation where animals concentrate on the same small patch of land every year. An example of this is a firebreak. In most rangeland ecosystems, fire-breaks are burnt annually as a precaution against accidental fires and they can occupy up-to 10% of the land on the farm (O'Connor *et al.* 2004). They are usually burnt in the early dry season to ensure they are in place and effective from the beginning of the fire season, and at this time the soil still retairns a little bit of moisture from the growing season (Savadogo *et* *al.* 2007). This moisture then promotes the fresh regrowth which has an attracting effect on the grazers soon after a new flush has re-sprouted (O'Connor *et al*. 2004).

Whether frequent repeated burning and grazing in one place is a good thing is still very much under debate, and probably depends on the particular environmental conditions, as well as the proportion of the landscape that is in this condition. Studies have indicated that if frequent burning is coupled with grazing, grazing tends to maintain the compositional diversity of grasses on frequently burnt patches (Collins *et al.* 1998; Augustine and Frank 2011). According to Hartnett *et al.* (1996), annual burning in grazed patches also resulted in increased plant diversity when compared to the four year burns on the Konza Praire Research Natural Area in the United States of America. Smith *et al.* (2012) also observed high grass richness, evenness and diversity in frequently burnt and grazed plots relative to unburnt plots at Kruger National Park in South Africa. However, just like in any other debate, there are two sides to the story, some people argue that intensive disturbance by fire and herbivory tends to exacerbate the effect of land degradation by removing too much above-ground biomass – in the long term having negative impacts on soil carbon balance (Yong-Zhong *et al.* 2005; Savadogo *et al.* 2007).

3.1.1 Grass community response to fire

Fire on its own has a homogenising effect on grass communities (Collins 1992; Collins and Smith 2006; Veen *et al.* 2008) by uniformly removing the above-ground biomass which then favours the dominance of just a few species when compared to unburnt grasslands (Veen *et al*. 2008). As a way of reducing the grass species diversity (Collins *et al.* 1998; Augustine and Frank 2011), frequent burning of South African mesic grasslands results in a grass community dominated by perennial grasses such as *Themeda triandra* and *Bothriochloa radicans* (Belsky 1992; Archibald and Bond 2004; Smith *et al.* 2012). These fire-climax systems are self-reinforcing: the species that dominate are all tall tussock grasses which are not palatable when fully grown, but which accumulate high fuel loads and tend to promote more fires (Archibald and Bond 2004). Thus frequent burning of grassland can result in uniform swards of highly-flammable (but not particularly palatable) grasses termed "black world" by Bond (2005).

Switching off fire in these systems can result in the grass becoming "moribund" and many fire-climax species will die out in these circumstances, being replaced by tall species such as *Cymbopogon validus* and *Alloteropsis semialata* (Everson and Tainton 1984; Fynn *et al.* 2005; Ghebrehiwot *et al.* 2006), which are also not particularly palatable (van Oudtshoorn 1999).

3.1.2 Grass ecosystem response to fire

Grassland fires tend to remove the aboveground herbaceous layer which exposes the ground surface to various external disturbances. The heat from the fire, together with the sunlight heat on an exposed ground tend to increase the soil temperature, hence lowering the moisture content of the soil through evaporation (Snyman 2003). Moreover, grassland fire also burns the soil organic matter which then promotes high soil compaction (even though not as severe) due to less pores between soil particles which is usually created by the soil organic matter (Snyman 2003). This also affects the infiltration ability of the soil structure as water will struggle to seep into the ground, therefore resulting in surface runoff (Johansen *et al.* 2001). Furthermore, burning of the soil organic matter may limit the nutrient supply to the soil and ultimately lower the above ground primary productivity of the grasses since the organic matter is important for returning soil nutrients (Snyman 2003). The standing biomass of the perennial grasses is also important in promoting soil infiltration capacity since the two are found to be linearly related (Snyman 2003). As a result of exposed ground surface due to a lag period of few weeks before the grass grows back (Russell-Smith *et al.* 2001) as well as increased surface runoff, therefore the process of soil erosion can get exacerbated which has been reported as leading to degradation (Johansen *et al.* 2001).

3.1.3 Grass community response to grazing

Grazing by herbivores tends to reduce the capacity of plants to photosynthesize and further disrupts their carbohydrate supply (Ash and McIvor 1998; Cullen *et al.* 2006). Therefore, grasses become resistant to grazing by adopting different strategies – either they develop adaptations that allow them to tolerate frequent defoliation, or they avoid defoliation by being unpalatable or hard to eat (Briske 1996; Cullen *et al.* 2006). With the tolerance mechanism, plants tend to grow back their leaves at relatively faster rates, a process called compensatory growth (Briske 1996). They achieve this through several physiological processes such as increasing carbon and nitrogen allocation to the leaves and undergoing compensatory photosynthesis as well as through meristematic activity (McNaughton 1983; Anderson and Briske 1995). This then results in an increase in Aboveground Net Primary Productivity (ANPP)

(Loeser *et al.* 2004). The avoidance mechanisms, however, are characterised by plants minimising the intensity or frequency of being defoliated by reducing plant palatability and accessibility (Anderson and Briske 1995). For instance, such grasses accumulate high levels of indigestible silica, cellulose and / or secondary compounds such as alkaloids to deter grazers (Briske 1996). Avoidance strategy can also be seen in some grasses through mechanical forms such as the toughening of leaves and the development of awns as seen in *Aristida* species (Briske 1996). If less grazed (avoidance mechanism) species are capable of growing faster than the highly grazed (tolerant) species, therefore the less grazed species will possess a competitive advantage within the grass community resulting in a landscape with decreased secondary productivity (Cullen *et al.* 2006). Moreover, as an alternative avoidance strategy, grass species such as *Cynodon* species undergo architectural plasticity by developing a decumbent or prostrate architecture in response to intensive grazing (Noy-Meir *et al.* 1989; Briske 1996) – i.e. by protecting some of their photosynthetic tissue by making it inaccessible. While this is also termed "avoidance" by Briske (1996), it results in very different leaf traits and plant attributes, and has a different impact on grazer communities from chemical avoidance, as these "lawn grass" plants are still palatable when grazed and it is not clear whether systems dominated by them have lowered secondary production (Hempson *et al.* 2015). Therefore these categorisations result in a number of different plant life-history strategies: 1) grasses being unpalatable to avoid herbivory (Briske 1996), 2) grasses being palatable, but tolerating a certain amount of herbivory through leaf replacement/compensatory growth (Anderson and Briske 1995), 3) grasses being palatable, but avoiding excessive herbivory by placing photosynthetic material somewhere where it cannot be accessed by herbivores (e.g below ± 1.5cm) (Hardy *et al.* 1997) and 4) palatable species which show no adaptations to grazing and cannot persist in heavily-grazed systems.

The impact of repeated heavy grazing on biodiversity and ecosystem function is still uncertain. Globally, light to moderate grazing intensities have been shown to increase (McNaughton 1984; Hartnett *et al.* 1996) the diversity and productivity of many grasslands, whereas heavy grazing may result in lower diversity and land degradation (Collins and Barber 1986). These contingent responses to grazing have been summarised by Milchunas *et al.* (1988) who indicates that evolutionary history (i.e. the type of grass species available) interacts with environment to determine grass communities under heavy grazing. Mowing experiments (surrogates to grazing) have been shown to enhance biodiversity in many grasslands (Collins *et* *al.* 1998); however, there is a possibility that frequent mowing can lead to low diversity. Moreover, heavily grazed communities seldom make up more than a small proportion of the landscape in most natural and managed ecosystems. Due to tall ungrazed veld having one suite of species, and short grazed veld having another, at a landscape scale perhaps biodiversity is best maintained with a mixture of both (Sala 1988).

Clearly heavily grazed grasslands are different from lightly grazed grasslands, but how are they different? Most of the work on grass community responses to grazing has focused on simple measures of diversity such as the abundance of certain species, species richness and the evenness in distribution of the species present in the community (calculated using Shannon-Weiner Index). Understanding the impacts of patchy grazing on grassland communities and landscape carrying capacities requires understanding the functional responses (Diaz *et al.* 2007) as well - that is mapping out the dominant grasses in terms of palatability and grazing tolerance. If we knew the order in which grass species were selected by grazing animals at a site, as well as the resistance that these species had to being grazed (how long they could persist in a heavily grazed state) then we would have a good indication of the sorts of grass communities that would emerge under heavy grazing.

3.1.4 Grass ecosystem response to grazing

In terms of ecosystem response, moderate to heavy grazing tends to increase the amount of bareground by removing the herbaceous layer on the ground (Pietola *et al.* 2005; Savadogo *et al*. 2007). The exposure of the ground surface together with the effect of trampling by herbivores may increase the compaction of the soil which may result in reduced water infiltration and low soil moisture due to increased surface runoff (Martínez and Zinck 2004). As a result, the reduction in soil moisture reduces the ANPP and vegetative cover (Belsky and Blumenthal 1997), creating positive feedback loops that further degrade both the soil structure and the plant community.

The response of ANPP however, is not straightforward. Grasses, unlike other life forms, have their growing points at the base of the plant, and are uniquely sensitive to self-shading. Thus the reduced vegetation cover mentioned above can also have a positive effect on grass productivity, as it increases light availability at the points of growth. The grazing optimisation hypothesis (under certain conditions) predicts a positive ANPP response to grazing (Hilbert *et al.* 1981; Belsky *et al.* 1993). It is defined as the increased response of primary productivity to grazing intensity where a threshold is reached at a moderate rate of herbivory (McNaughton 1979; Hilbert *et al.* 1981; De Mazancourt *et al.* 1999; Loeser *et al*. 2004). This is attained through nutrient cycling in the form of dung deposition (Belsky 1986; Augustine and Frank 2001; Veen *et al.* 2008) and increased plant growth as a result of greater light availability to tissue previously shaded, through the removal of either older plant matter or plant matter of competing plants (McNaughton 1979; De Mazancourt *et al.* 1998; Anderson *et al.* 2007). The measure of this response of ANPP to grazing is largely known as overcompensation, which is a response of plants to defoliation by herbivores, where the plant either partially or completely compensates for the loss of biomass and the overall response results in an increase of productivity (Farraro and Oesterheld 2002; Loeser *et al*. 2004).

3.2 Aim

This chapter of my project was aimed at looking at the functioning of firebreaks under the pressure of both a decade of annual burns and of constant grazing in tall Sourveld grassland.

3.3 Objectives

The objectives of the study in this section were:

1) To quantify long-term impacts of repeated fires and grazing on grass community composition using firebreaks.
2) To quantify the long-term impacts of repeated fire and grazing on system function (in terms of quantifying percentage bareground, soil moisture, soil compaction and infiltration rates) and grass productivity (ANPP).

3.4 Hypotheses

1) I hypothesized that the firebreak was going to have more grazer presence relative to the adjacent unburnt control, due to short and nutritious grass growing on the firebreaks.
2) I hypothesized that the grassland community on the firebreak was going to be different in species composition relative to the adjacent unburnt matrix: that it would have lower diversity and a unique assemblage of species.

3) In terms of function, I hypothesized more signs of degradation on the fire-break (for example, more bare-soil, high soil compaction, less water infiltration and less soil moisture relative to the unburnt matrix due to the long-term impact of fire-grazing interactions.
4) In terms of productivity, I hypothesized less productivity on the firebreaks due to degradation and overgrazing

3.5 Materials and Methods

3.5.1 Location of the study site

The firebreaks at the studied site (Figure 3.1) represented the long-term impact of both fire and grazing on grass community. They were about 20m wide and they had been burnt annually for at least the last 10 years (Stephan du Toit: pers. com.). During the sampling period the sampled firebreak on the left hand side of the experimental burnt image (described in Chapter 2) in Figure 3.1 together with the adjacent unburnt site were divided into 9 transects (3 per each topographic position) starting from the bottom, middle and to the top (transect 3.1) of the slope to account for topographic influences. Those 3 x 3 transects on each of the two treatments (burnt and the adjacent unburnt) were all 16m long in order to survey a total of 48m of transect (3 x 16m) at each topographic position. In going forth, these three topographic positions along the slope are further referred to as plots (therefore, each plot consisting of 3 16m transects).

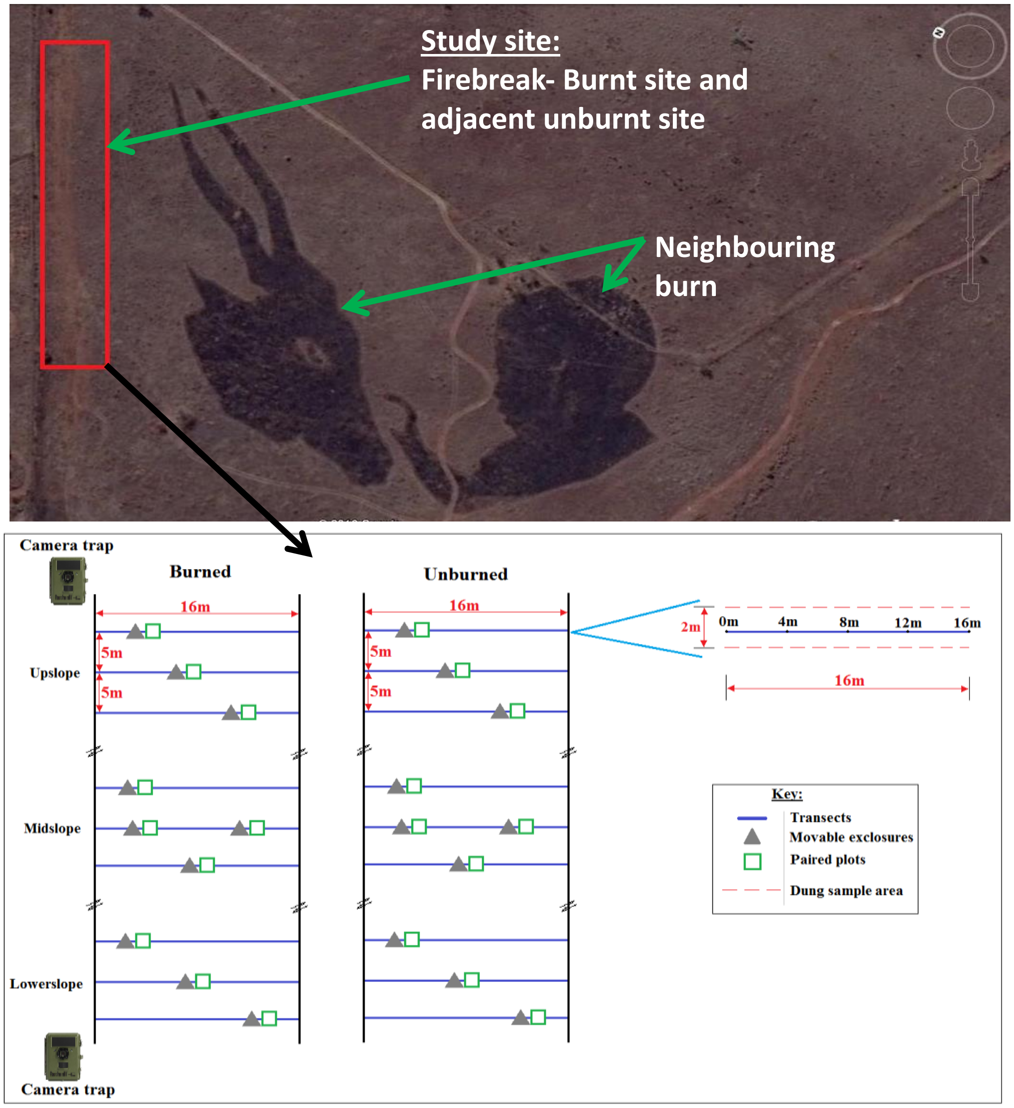

Figure 3.1: The position of the fire-break and the adjacent unburnt control situated on the left of the 5 hectare neighbouring burn (described in Chapter 2) both pointed by green arrows (a). The black arrow is pointing at the schematic diagram (b) describing the experimental set-up of a total of 20 exclosures alongside paired plots along nine transects on both burnt and unburnt sites. Each transect measuring 16m long on both sites. Positions of the exclosures and paired plots were changed monthly. Dung samples were collected along each transect within a 4m belt transect (2m on either side of the transect). The camera traps were stationed as shown to record grazer presence on both the firebreak and the adjacent unburnt matrix.

3.5.2 Grazer presence on the firebreak

Within a 4m belt transect (2m on either side of the transect) along each of the nine transects dung identification was done and the number of dung piles were counted, both on the firebreak and on the unburnt control. After being recorded, the dung was crushed or removed from the sites to prevent double sampling. The presence of a certain species of dung was taken as an indication that that particular species had been foraging at the site (Sensenig 2009) (Figure 3.1b).

Although dung counts are appropriate for comparing species presence at different sites at the same time, they are not good for tracking changes over time, because seasonal patterns of rainfall and dung beetle activity alter the decomposition rates (Barnes 2001, see also Chapter 2). Aiding the use of dung counts, two camera traps were installed at the study site, in January 2016. One camera was placed at the bottom of the slope facing across and up the slope and another at the top of the slope facing across and down (Figure 3.1b). The field of view (FOV) of the cameras facing both on and off the firebreak was demarcated on the ground and measured in m^2 (as done in Chapter 2). The camera traps observed a total burned area of $4132m^2$ and a total unburned area of $4544m^2$. The camera-traps were set to take photographs in 15minute intervals from 6:00-18:00 daily. These photographs were used to visually measure grazer presence by recording the number of the individuals of a certain species present at either site during the period of the study. Only the grazers inside the demarcated area of the field of view on both the firebreak and the unburnt control were recorded in order to have a quantifiable measure of grazer presence per unit area per unit time (kg grazers / area /time).

Although the sensors on camera traps were set at the lowest sensitivity to avoid movement-triggered images they still occurred, but were excluded from the analysis. The total grazer biomass recorded on each on each treatment over the study period in kg/km^2 was calculated by multiplying the number of individuals per species by the average body mass of that specific species and dividing that by the FOV of the camera-trap (i.e. $\sum[(N \text{ x average species mass in kg})]/ FOV$). Since the numbers of images taken by each camera were equal, the total herbivore biomass per day was calculated by summing the 15 minute biomass values for each day for each camera. Monthly grazer counts per km^2 were calculated by summing the daily averages per month. Finally, a grazer selectivity index (as seen in Sensenig *et al.* (2010) and explained in Chapter 2) for the burnt site was created for each species for the duration of the study, summing the monthly data and all cameras grouped together as replicates. This was done by dividing the summed monthly counts per km^2 for the burnt treatment by the sum of the monthly counts per km^2 for the burnt and for the unburnt treatment (∑monthly counts per km^2 in burnt)/ (∑monthly counts per km^2 in burnt) + ∑monthly counts per km^2 in unburnt). The purpose for creating this index was to determine grazing preference of the herbivores and a value greater than 0.5 indicates preference for the burnt site for that species.

3.5.3 Grass community composition

To assess grass community composition and basal cover a levy bridge (Levy and Madden 1933; Everson and Clarke 1987) was laid down vertically every 1m along all horizontal transects, both on and off the firebreak. I then recorded all the grass and forb species touching any of the 10 pins of the levy bridge. Recording both grasses and forbs was done in order to obtain the percentage abundance for each grass species relative to the total herbaceous cover (grasses and forbs). This method gave a total of 1440 records (10pins x 16m x 3 plots) for each treatment – many of which were bare ground.

3.5.4 The functioning of the firebreaks

To investigate the functioning of the firebreaks, I compared four classic measures landscape functioning (percentage bareground, soil compaction, water infiltration and soil moisture) on the firebreak relative to the adjacent unburnt matrix. All these measurements were taken late in the dry season to avoid bias as the measurements when the soil was wet after the rains would have been different.

The above mentioned levy-bridge was also used to quantify the percentage bareground both on and off the firebreak. I used the percentage of pins that were touching bareground instead of the vegetation as a measure of bareground.

Soil compaction was quantified using a Dynamic Cone Penetrometer (DCP) which measures the penetration index (PI) in by dropping a 10 kg weight from a specific height of 575mm and then obtaining the depth penetrated by the cone in millimetres per blow (mm per blow) as described by (Herrick and Jones (2002) and (Mooney and Rinehart (2007). At each spot, the DCP was dropped 2 times on the same position and the average of those 2 measurements was taken. There was no need for dropping the DCP several times on one spot because unlike tree roots grass roots are generally located close to the surface of the soil structure (Belsky *et al.* 1989). This was done every 1m along each transect both on and off the firebreak. A low PI represented a high soil compaction because it meant that the ground was too hard for the DCP to penetrate it.

The infiltration rate was investigated using a modified single ring infiltrometer as illustrated by Dean and Yeaton (1993), comprising of a 425g can with the diameter of 75mm, used alongside a stop watch. The can was open at both ends to allow water to dissipate into the ground, whereas the stopwatch was used for recording the time taken by a known amount of water to seep into the ground. At each of the three landscape positions (3 plots) three replicates of infiltration rate were measured on the firebreak as well as on the control. The can was pushed gently on the ground to avoid breaking the surface soil structure, and then 200ml of water was poured into the can in 10ml intervals. This was done to avoid creating too much water pressure which was going to result in increased surface run-off instead of water seeping downwards. Also to minimise run-off these measurements were done on a bit flatter surfaces as even though my site was on a slope. In every 10ml interval, the time taken for the water to seep into the ground was recorded. The infiltration rate over time was then calculated as the time taken for 200ml of water to infiltrate into the ground for each of the three transects on both the firebreak and the unburnt control.

A soil auger was used to collect soil samples of about 300g on each of the nine 16m transects making 3 replicates per landscape position both on and of the firebreak. Soon after collecting, the soil samples were immediately put into plastic Ziploc bags for further analysis later. In the lab, those samples were weighed (to obtain wet-mass) then transferred into brown paper bags, and dried for 72 hours in an oven set at 70°C according to Dean and Yeaton (1993). Then after, the samples were weighed again to obtain dry mass. Soil moisture content was then calculated as a percentage of the weight difference relative to the dry weight (i.e. on a mass basis).

3.5.5 Grass Annual Net Primary Productivity (ANPP)

These data were collected over a period of six months (November 2015- May 2016) on a drought year (the rains only started coming in January 2016) by my colleague Alekzandra Szewczuk for her Honours Project, therefore her willingness to share this crucial information is duly noted. They were collected on the same site and transects I collected the rest of my data (Figure 3.1b). To examine the Annual Net Primary Productivity (ANPP) she used methods described by Sala and Austin (2000) and used by Knapp *et al.* (2012) which account for the off-take by grazing herbivores but using paired moveable exclosures to estimate monthly off-take.

A total of twenty movable exclosures (MEs) with corresponding paired (unfenced) plots (Pps) were used to quantify the ANPP over roughly monthly time intervals during the growing season of 2015 to 2016 (Figure 3b). Out of these twenty exclosures, there were 10 on each treatment (firebreak and the adjacent unburnt control) (Figure 3b). The MEs were pyramid shaped with a base of 0.16 m^2 (40 cm x 40 cm) and 40 cm in height and the corresponding Pps also had an area of 0.16m^2.

Every month the MEs were placed in a new location and an associated paired plot was located nearby – aiming to mimic the species composition and biomass to that in the associated ME plot. The MEs and Pps were repositioned every month along or within the 5m width of the transects, to reduce errors as a result of oversampling (Knapp *et al.* 2012). On setting up the MEs and the Pps, the aboveground biomass of the paired plots was clipped, before they were moved to a new location. In the following monthly interval the aboveground biomass of the MEs was clipped. Upon clipping, only grass species were clipped and collected, woody species and forb species were excluded from this particular study.

For the adjacent unburnt control the live biomass was separated from the dead biomass under the assumption that the dead biomass was growth from the previous growing season (Loeser *et al.* 2004; Knapp *et al.* 2012; Everson and Everson 2016). While for the burnt sites, it was assumed that all growth present was growth from current season. The collected samples were then oven dried at 70°C for roughly 12 hours and weighed.

3.6 Data Analysis

All data were analysed using R Statistical programme, Version 3.4.0 and significance was determined when $p < 0.05$. For all analyses below (with the exception of the camera data) I had three transects (16m long) at each of the three landscape positions on both the firebreaks and the adjacent unburnt control.

3.6.1 Grazer presence analysis

The first hypothesis of this chapter which stated that there was going to be more grazer presence on the firebreak relative to the adjacent unburnt matrix was tested as follows. The total dung counts per species over the study period, and total grazer biomass density from the camera data were all calculated for both the burnt and unburnt treatments. A non-paired t-test was used to compare the dung counts between the two treatments (burnt vs. unburnt), with nine transects on each treatment as replicates. As for the daily grazer biomass from the camera-trap data, a non-paired Wilcoxon signed rank test was conducted from the two sites. The data was zero inflated even when it was summed to a monthly time step because many of the photographs did not have any animals recorded at all. Therefore, it was not ideal to conduct a parametric analysis on this data. This analysis was done on data from both cameras grouped together as well as the monthly data as replicates. The mean grazer selectivity was determined to assess the overall grazer preference.

3.6.2 Grass community composition analysis

To answer the second hypothesis that the grassland community on the firebreak was different in species composition relative to the adjacent unburnt matrix: that it would have lower diversity, but a unique assemblage of species, the following was done.

The number of unique species and species diversity were all calculated and compared between the firebreak and the adjacent landscape. The grass species diversity (which accounts for evenness) was assessed and compared between the two treatments using a Shannon-Weiner index which is calculated using the equation ($H' = -\Sigma p_i \ln p_i$) where, pi is the relative abundance or basal cover of species i in each treatment (Magurran 1988; Hartnett *et al.* 1996). Species compositional differences between the two sites (according to the first hypothesis) were compared using a Canonical Correspondence Analysis (CCA) explained by (ter Braak 1986) and this analysis was run using “vegan 2.4-1” package in R. This method is a numerical technique used to assess how species composition changes in relation to environmental variables and also most importantly the relationship between different environmental variables (Hill *et al.* 2016) – thus extending weighted averaging to the simultaneous analysis of many species and environmental variables (ter Braak and Verdonschot 1995). Therefore, data containing the environmental variables (bareground, infiltration rates, soil moisture and penetration index and treatment data (treatment = firebreak or unburnt control, topography = bottom, mid and top slope) were included in the analysis. The CCA method works on the collected field data on abundances or occurrences (e.g. counts or proportions of individuals) of species and data on environmental variables at different sites and therefore, extracts from the measured environmental variables synthetic gradients in the form of ordination axes that maximises the niche separation among species (ter Braak and Verdonschot 1995). Therefore, sites are plotted in multidimensional space according to how similar they are in terms of species composition (abundance of different species). The CCA begins the ordination by constraining the environmental variables as the first few axes (n=number of environmental variables) and then completes the projection with the above mentioned “synthetic gradients”. Before importing the two spreadsheets (species data and environmental variables data) into R, the species proportions of occurrence or abundance in each site were calculated and they were centred and scaled. The average value per plot (set of 3 transects in each landscape position) was used for the environmental variables. Treatment was entered as a binomial variable (1 = unburnt, 0 = firebreak), and topography was an ordinal variable where plots, 1, 2 and 3 were situated at the bottom, mid and top of the slope, respectively.

A cluster analysis was also performed in R on raw data to separate grass species according to their distribution, either on the firebreak or on the unburnt control. This was done using the “hclust” function which uses a set of Bray-Curtis dissimilarities in a certain number of objects being clustered to perform a hierarchical cluster analysis. As described by (Murtagh and Legendre 2011 and in the R program), the function firstly assigns each object to its own cluster and then the algorithm proceeds iteratively, at each stage joining the two most similar clusters, continuing until there is just a single cluster. As a result, the dissimilarity of the species – site clusters is joined together hierarchically in the form of a dendrogram.

3.6.3 Functioning of the firebreaks analysis

To test the third hypothesis which stated that the firebreak was to show more signs of degradation; data were first tested for normality using Normal Probability Plots (QQ plots) and histograms. For data which followed a normal distribution (percentage bareground and soil moisture) and data which did not follow a normal distribution (soil compaction and infiltration rates) I analysed them using a parametric non- paired t-test and a nonparametric Wilcoxon signed rank test respectively, to compare between the firebreak and the unburnt control (n of 6 because I averaged the data from each plot to avoid pseudo-replication). The effect of the slope on those four parameters was investigated using interaction plots in the “stats” package (Version 3.4.0) in R.

3.6.4 ANPP analysis

For the fourth and final hypothesis for this chapter which stated that there was going to be less productivity (ANPP) on the firebreak due to degradation and overgrazing, the following was done.

After oven drying, the weight of the grass from the Pps was subtracted from that from the MEs to give a total of 10 monthly measures of ANPP for each plot for the six months of the experimental period (a total of 60 records). It was therefore possible for the calculated ANPP measures to be negative (if the weight of the grass in the Pps at the beginning of the month was greater than that at the end of the month in the MEs). To calculate monthly ANPP, the 10 records per treatment were treated as replicates, hence averaged. However, to calculate the annual ANPP, the 6 months values for each replicate were first summed, and then averaged per site (i.e. total annual ANPP= $\Sigma_{i = 1:10} (\Sigma_{x = 1:6} [(ME_{xi} - Pp_{xi})])/n$, where x is the month and i is the replicate and n is the total number of replicates (10). The total annual ANPP for the burnt and unburnt sites were therefore analysed using a non-paired t-test (n = 20 ANPP values from 10 quadrats on each treatment).

3.7 Results

3.7.1 Grazer utilisation of the burns

From a non-paired t-test, there was no significant difference in dung counts between the firebreak and the unburnt control (*p*=0.55), which was not according to the expectations. However, the camera trap data showed plainly that all grazer species spent more time on the burnt firebreak than on the unburnt control (Table 3.1). The burnt site (n=316) had almost double the total number of grazer visitations than the unburnt site (n=160) (Table 3.1), with the short-grass grazers (wildebeest and hartebeest) showing the strongest response with a selectivity index over 0.9 for both species. Surprisingly although they are considered short grass specialists (Waldram *et al.* 2008) the blesbok had selectivity values similar to zebra (0.78 and 0.81 respectively), but still higher than impala and gemsbok (0.70 and 0.69) (Table 3.1). Moreover, the total grazer biomass on the firebreak (23208kg/km^2) was double that of the unburned (11435kg/km^2) site (Table 3.1) over the five months, and the average daily grazer biomass recorded at the two sites was significantly different ($p < 0.05$; the Wilcoxon signed rank test).

Table 3.1: Total number of grazers recorded on each treatment; grazer mass per km^2 and grazer selectivity for the firebreak, based on camera trap data from January to May 2016. Grazer selectivity is quantified as the kg/km^2 on the firebreak/ (kg/km^2 firebreak + kg/km^2 unburned): values > 0.5 indicate preference for the firebreak.

	Grazer counts		**Biomass (kg/km$^{2)}$**		**Grazer selectivity for firebreak**
	Burnt	**Unburnt**	**Burnt**	**Unburnt**	
Hartebeest	55	2	1743	366	0.966
Blesbok	36	11	994	479	0.754
Impala	28	13	614	226	0.740
Wildebeest	17	2	1504	98	0.845
Zebra	178	131	18288	10204	0.564
Gemsbok	2	1	65	61	0.790
Total	**316**	**160**	**23208**	**11435**	

3.7.2 Grass community composition

A total of 25 grass species were recorded at both sites (firebreak and the adjacent unburnt control) combined. Moreover, 4 species were only found on the firebreak (*Aristida conjesta* sub. *barbicollis*, *Eragrostis gummiflua*, *Eragrostis patentipilosa* and *Trichoneura grandiglumis*) and 3 species were only found on the unburned area (*Digitaria diagonalis, Triraphis andropogonoides* and *Urelytrium agropyroides*). In addition to having more unique species, the firebreak also appeared to be more diverse than the unburnt control (Shannon Wiener Index: 2.015 versus 1.828). The top three species on the firebreak were *Eragrostis chloromelas* (17.7%), *Setaria sphacelata* (15.0%) and *Heteropogon contortus* (10.5%), making up 43.2% of the total basal cover. In contrast, the top three species on the unburnt control were *Setaria sphacelata* (28.3%), Setaria incrassata (9.6%) and *Trachypogon spicatus* (8.1%), making up 46% of basal cover. Overall the firebreak also had less total herbaceous basal cover of 41% compared to the 56% on the adjacent unburnt site.

The effect of treatment was clear from the ordination results. The first axis (treatment) of the CCA accounted for 49% (Table 3.2) of the variation and was clearly associated with both treatment and with the four environmental variables measured above. *Aristida conjesta* (sub. *conjesta* and *barbicolis*) , *Themeda triandra* and *Eragrostis partentipilosa* and *Cynodon dactylon* were species associated with the firebreak treatments, as well as increased bareground, and these species correlated negatively with soil moisture, penetration index, and infiltration rates (Figure 3.2) In contrast *Digitaria diagornalis*, *Urelytrium agropyroides* and *Triraphis andropogonoides* were associated with the unburned matrix, low bare ground, and positive soil moisture and infiltration scores. (Table 3.2, Figure 3.2). The second axis of the CCA accounted for about 21% of the variation and appeared to be related to the slope (Figure 3.2). Sites at the top of the slope (transect 3) were represented by *Aristida congesta subs.barbicolis* and *Eragrostis patentipilosa*, with *Brachiaria serrata*, *Microchloa caffra* and *Eragrostis* species occurring towards the bottom. (Table 3.3, Figure 3.2). In total the first two axes accounted for 70% of the variation in species composition across the 6 sample sites. The relationships among the environmental variables were such that, the soil moisture and bareground were exactly opposite, and that the increase in soil moisture, infiltration rate and the penetration index pulled towards the unburnt site whereas only the increase in bareground pulled towards the firebreak.

Table 3.2: Results from the canonical correspondence analysis showing the principal component axes constrained by the five explanatory variables. The first two axes explain ~70% of the variation

Variable	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**	**Axis 5**
Eigenvalues	0.3603	0.1527	0.1150	0.0772	0.0489
Cumulative Proportion Explained	0.4908	0.6989	0.8556	0.9334	1.0000

Table 3.3: Grass species scores from the canonical correspondence analysis ordered in terms of their scores in the first constrained principal component (i.e. from those preferring the control (less frequently burnt) habitat to those preferring the firebreak.

Species	***Spp. abbr***	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**	**Axis 5**
Urelytrium agropyroides	*Ure.arg*	1.3661	-0.4302	0.21954	-0.9482	1.62087
Triraphis andropogonoides	*Tri.and*	1.3322	-0.3986	-0.0099	0.50749	0.18418
Digitaria diagonalis	*Dig.dia*	1.3073	-0.3755	-0.1784	1.5772	-0.8716
Andropogon schirensis	*And.sch*	0.9534	-0.1336	-0.2397	-0.4454	0.07685
Setaria incrassata	*Set.inc*	0.8695	-0.0532	-0.3251	0.13159	-0.2568
Diheterepogon amplectens	*Dih.amp*	0.781	-0.0676	0.28834	-0.0252	-0.0059
Trachypogon spicatus	*Tra.spi*	0.5632	-0.1532	-0.0057	-0.1032	0.07289
Melinis repens	*Mel.rep*	0.5545	0.1709	-0.0544	0.1678	0.13252
Eragrostis racemosa	*Era.rac*	0.2405	0.02375	0.28986	0.03333	0.07014
Brachiaria serrata	*Bra.ser*	0.2358	0.20098	0.1627	-0.0596	0.28291
Setaria sphacelata	*Set.sph*	0.1841	-0.2052	0.03862	-0.1771	-0.1004
Aristida canescens	*Ari.can*	-0.1446	0.68139	-0.2008	0.01694	-0.2771
Heteropogon contortus	*Het.con*	-0.284	0.15797	0.0002	0.15241	0.04796
Eustachys paspaloides	*Eus.pas*	-0.3757	-0.271	-0.7039	-0.9159	-0.8127
Hyparrhenia hirta	*Hyp.hir*	-0.4076	0.09277	-0.5724	-0.1259	0.38537
Microchloa caffra	*Mic.caf*	-0.4518	0.94838	-0.3359	-0.0562	0.02812
Eragrostis chloromelas	*Era.chl*	-0.4709	0.03964	-0.1571	0.17893	-0.0836
Eragrostis gummiflua	*Era.gum*	-0.4774	0.60393	1.95694	-0.0734	-0.3623
Trichoneura grandiglumis	*Tri.gra*	-0.4774	0.60393	1.95694	-0.0734	-0.3623
Eragrostis curvula	*Era.cur*	-0.6918	0.49107	-0.2292	0.1489	0.21456
Cymbopogon caesius	*Cym.cae*	-0.7087	-0.2793	-0.6399	-0.28	-0.1709
Cynodon dactylon	*Cyn.dac*	-0.7384	-0.4012	0.57758	-0.2236	-0.3102
Themeda triandra	*The.tri*	-0.7765	-0.0616	0.32071	0.0279	-0.006
Aristida conjesta	*Ari.conj*	-0.9653	-0.3522	0.19152	0.21654	0.20386

Eragrostis patentipilosa	*Era.pat*	-1.2275	-1.1602	-0.3894	0.22589	0.29452
Aristida (sub) barbicollis	*Ari.bar*	-1.3343	-1.7812	-0.2615	0.08445	0.11967

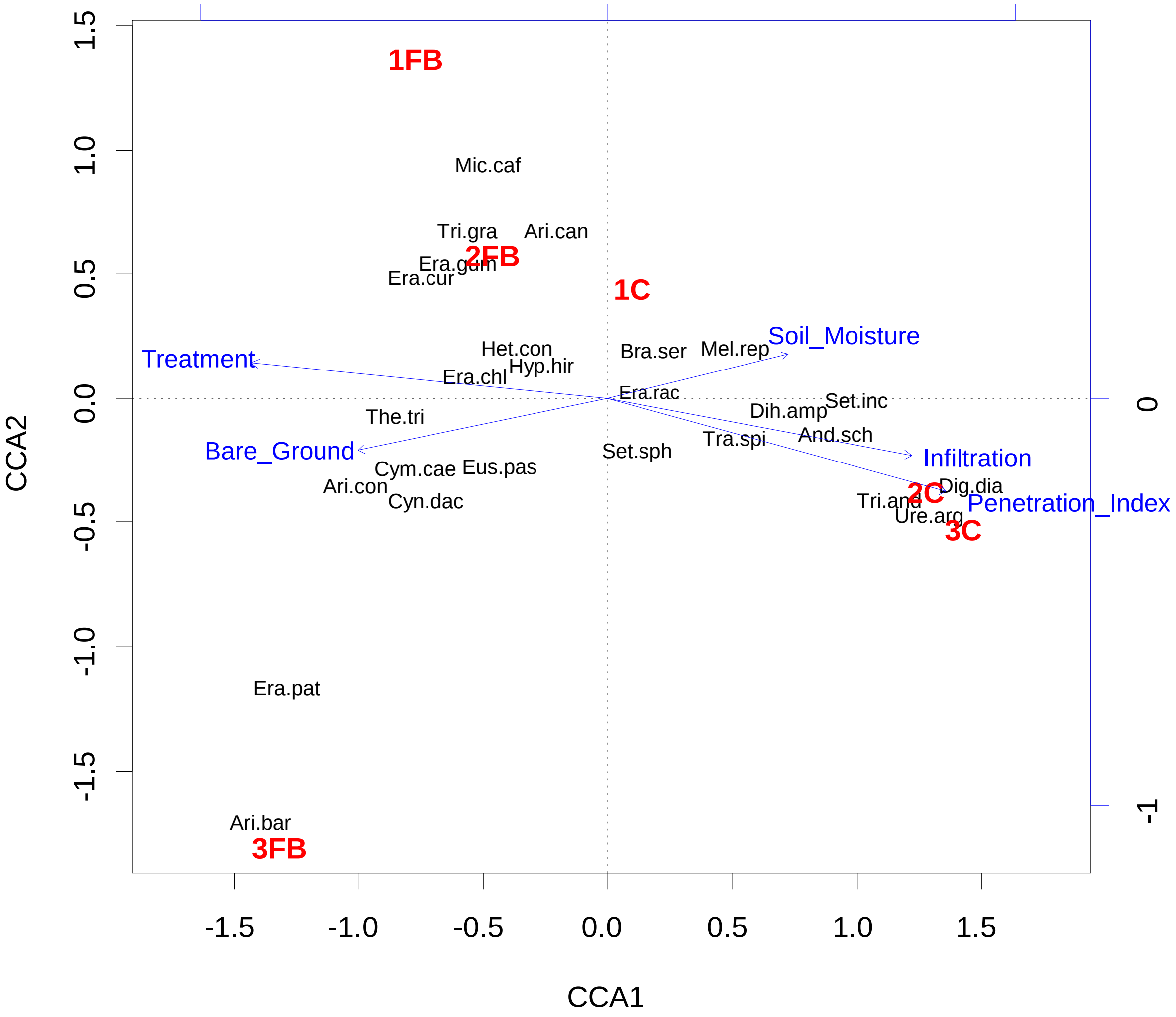

Figure 3.2: Ordination plot from the canonical correspondence analysis of grass species composition relative to the environmental variables. The abbreviated grass species names shown in black are written in full in Table 3.3 and the environmental variables in explaining the species composition are shown with blue arrows and the length and direction of the arrows indicate the correlation and the importance relative to the other axes. The first axis CCA1) is associated with the Treatment (1 = unburnt, 0 = firebreak),

whereas the second axis (CCA2) is associated with slope (site 3, site 2 and site 1 in red: being the top, middle and the bottom of the slope, respectively).

The effect of landscape position appeared to be stronger on the firebreak than on the unburned control, with the species separating out more strongly in this portion of the graph (Figure 3.2). Moreover, the difference between treatments was less clear at the bottom of the slope for the Firebreak site, with “F1” site not clearly separating from the unburnt sites in a cluster analysis (Figure 3.3). This might relate to the increased soil moisture on the firebreak at the bottom of the slope therefore making it similar to the unburnt plots with increased soil moisture (Figure 3.5)

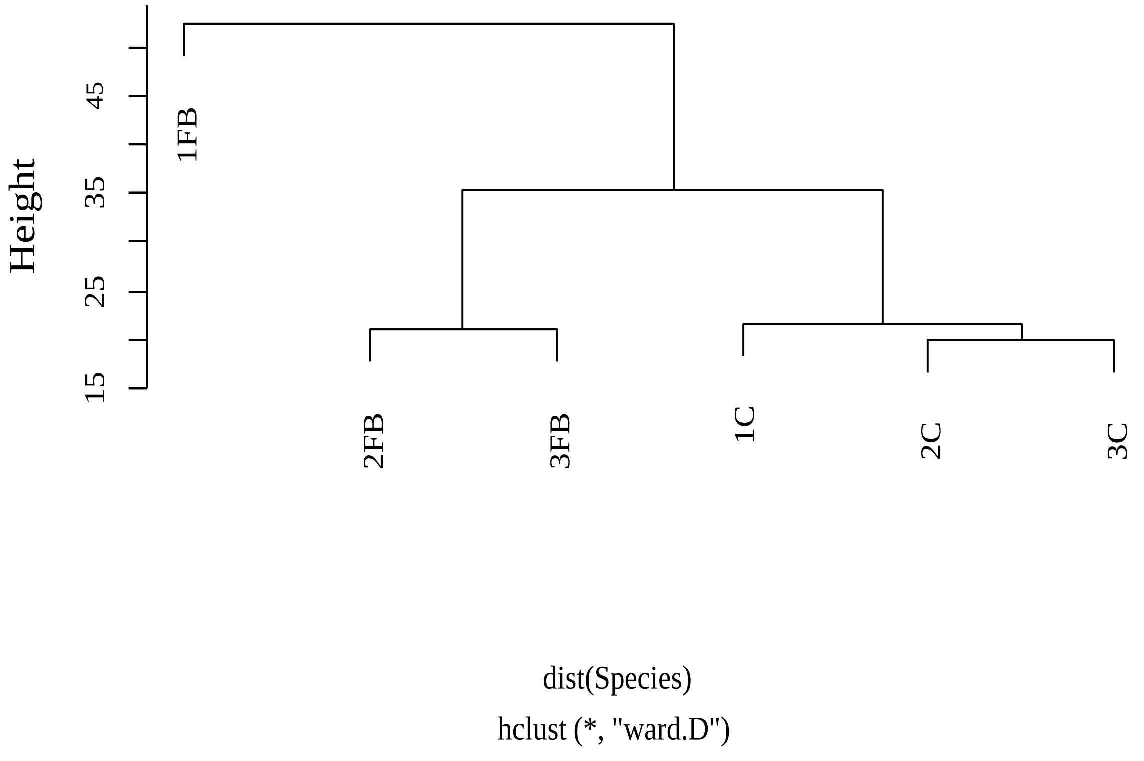

Figure 3.3: A Cluster dendrogram showing the dissimilarities of species distribution between the firebreak (F) and the adjacent unburnt control (C).

3.7.3 The functioning of the firebreaks

Three of the four measures of landscape functioning that I used indicated that the firebreaks were more degraded than the unburned matrix. The percentage bareground was significantly higher on the FB (Figure 3.4a) relative to the adjacent unburnt Control (~20% vs. ~14%: $t_{3.997} = 3.6433$, $p = 0.02$). The Firebreak had a significantly lower (~10mm/blow vs. 20mm/blow) Penetration index (Figure 3.4b) indicating a higher soil compaction relative to the Unburnt (Wilcoxon signed rank test: W = 1490, $p < 0.05$, n = 81). Moreover, infiltration rates and soil moisture, were both lower (~ 4ml/min vs. ~10ml/min and ~6% vs. 8%, respectively) on the Firebreak relative to the Unburnt control (Figure 3.3c and 3.3d, respectively), although the difference was not significant in terms of soil moisture (Wilcoxon signed rank test: W = 27, $p < 0.05$, n = 18 and t-test: $t_{9.407} = -1.0658$, $p = 0.31$, respectively).

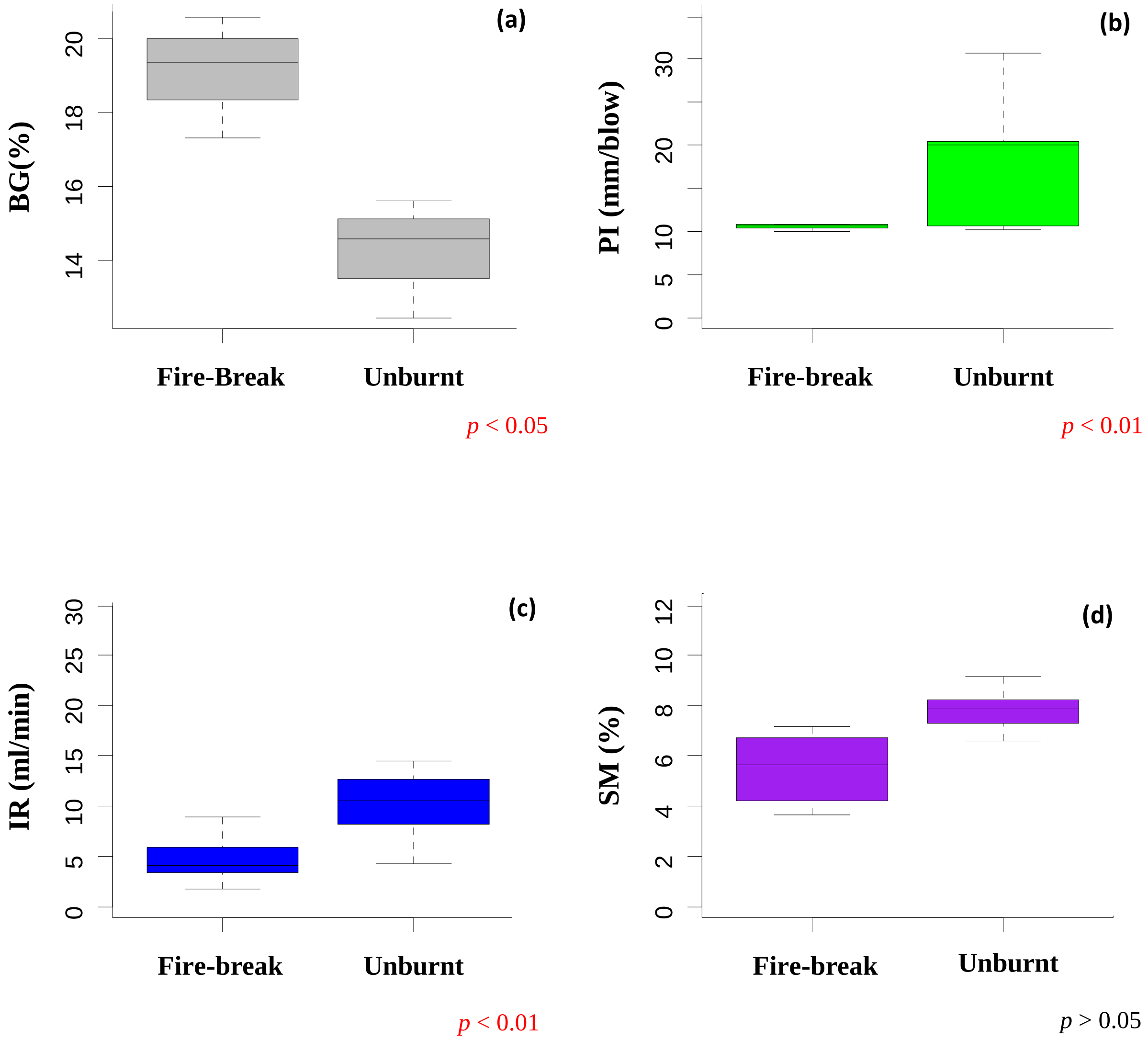

Figure 3.4: The investigated four signs of poor landscape functioning (percentage bareground, soil compaction in terms of penetration index, infiltration rates and gravimetric percentage soil moisture) on the firebreak relative to the adjacent unburnt matrix. (a) represents percentage Bareground (BG in %), (b) Penetration index (PI in mm/blow) which is an inverse measure of soil compaction, (c) Infiltration rates (IR in ml/min) and (d) gravimetric Soil moisture (SM in %) between the two treatments (Firebreak and the adjacent Unburnt control). The *p*-values less than 0.05 show a significant difference between the two treatments and vice-versa.

I found that the sites at the bottom of the slope generally had more compact soil and lower infiltration rates than sites further up the slope (Figure 3.5b and c), but they also had less bare ground (Figure 3.5a). Interestingly the treatment effect on soil moisture varied from the top of the slope to the bottom, with the firebreak having wetter soils at the bottom of the slope, and drier soils on the top of the slope (Figure 3.5d). I could not do statistical tests on these data as I did not have enough replicates.

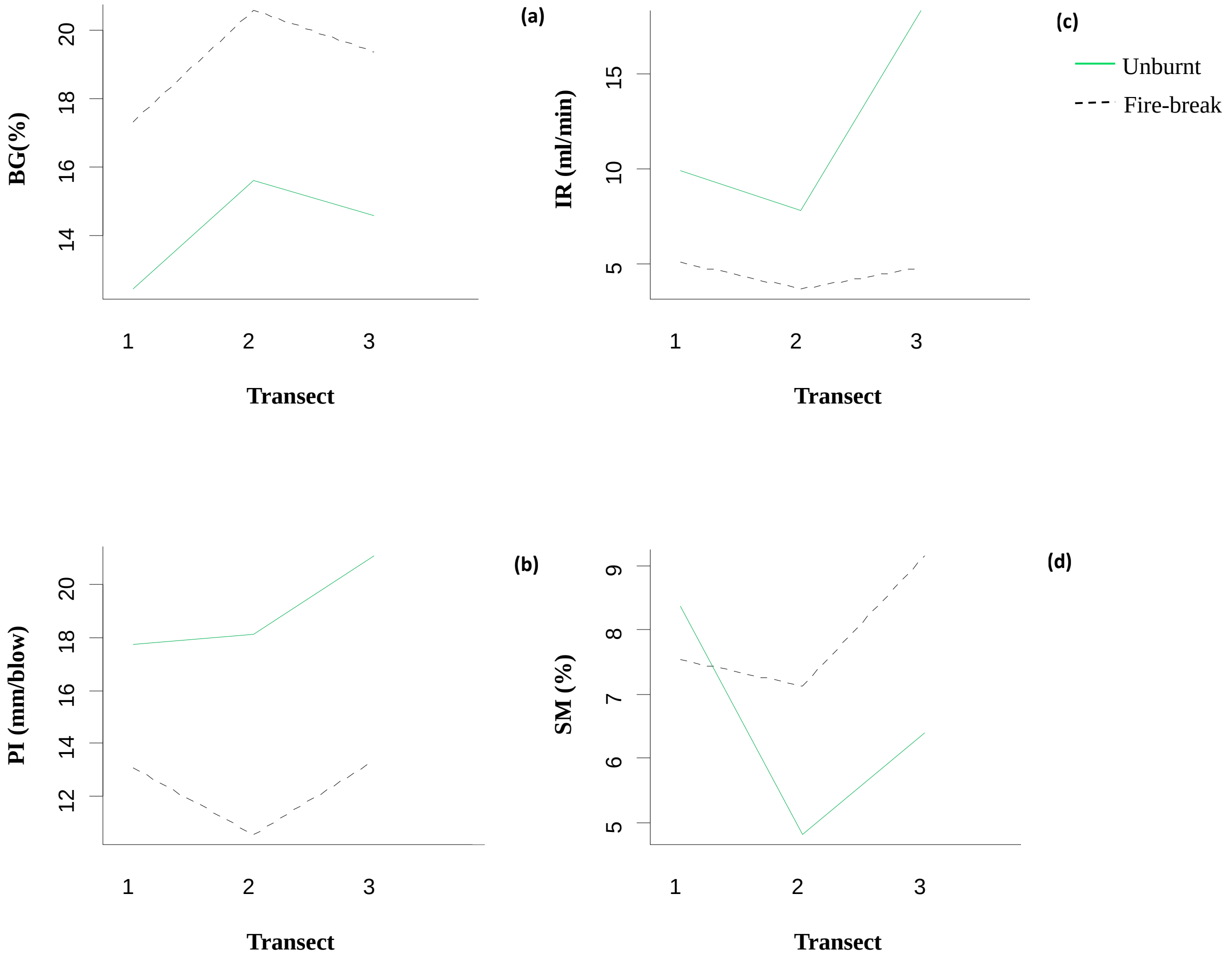

Figure 3.5: Interaction plots showing the effect of the slope (transects) on percentage bareground (BG in %), penetration index (PI in mm/blow) as a measure of soil compaction, infiltration rates (IR in ml/min) and the gravimetric soil moisture (SM in %). Transect 1, 2 and 3 ran across the bottom, middle and the top of the slope respectively. The p-values less than 0.05 show a significant difference between the two treatments and vice-versa.

3.7.4 Grass Annual Net Primary Productivity (ANPP)

The average annual ANPP of the annually burnt firebreak was 146.42 g/m^2 which differed significantly (T-test: $t_{117.45} = 3.568$, $p < 0.05$) from the 56.47 g/m^2 of the adjacent unburnt matrix, with the annually burnt firebreak yielding a significantly higher total annual ANPP (Figure 3.6), despite this being a very low rainfall year (55% of the annual average precipitation fell during the 2015-2016 rainy season).

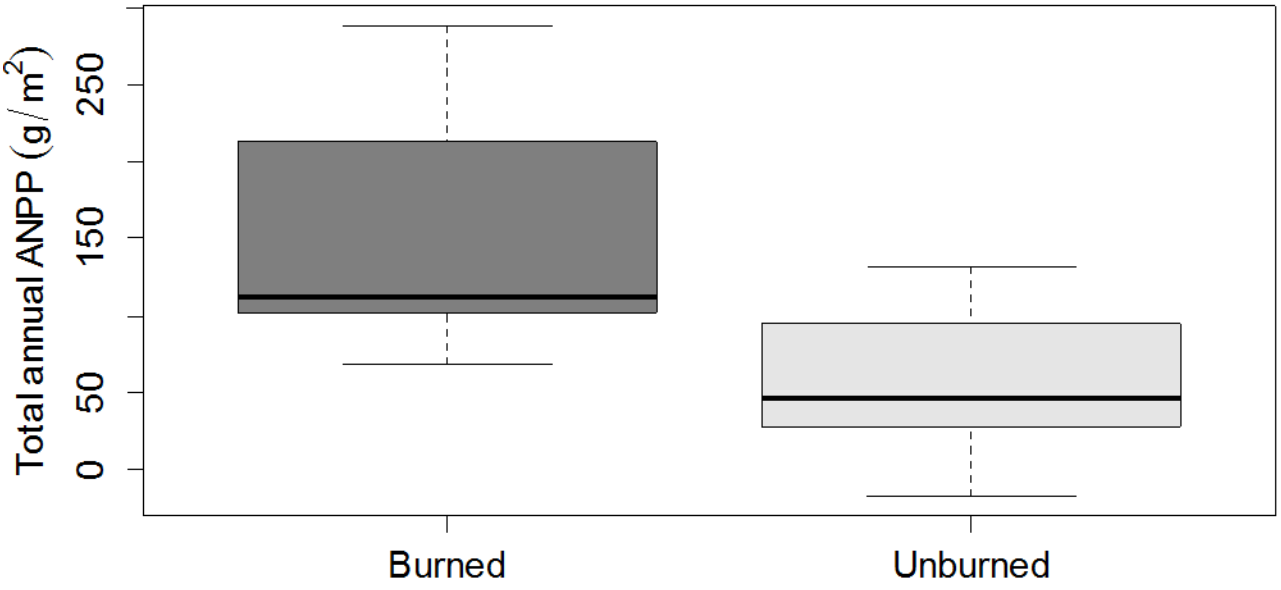

Figure 3.6: The total annual ANPP response of grasses of Highveld grassland to two different fire-grazer treatments over six months (November 2015- May 2016). The burned site is an annually burnt firebreak experiencing heavy grazing and the unburned site is an adjacent unburnt control. Results are a boxplot of the summed monthly ANPP calculated from 10 replicated matched exclosure pairs on each treatment. There is a significant difference between the ANPP of the two sites ($t_{117.45} = 3.568$, $p < 0.05$).

The monthly ANPP of the burned site increased for most of the growing season before decreasing again towards the latter half of the season, while the monthly ANPP of the unburnt site fluctuated throughout the season (Figure 3.7).

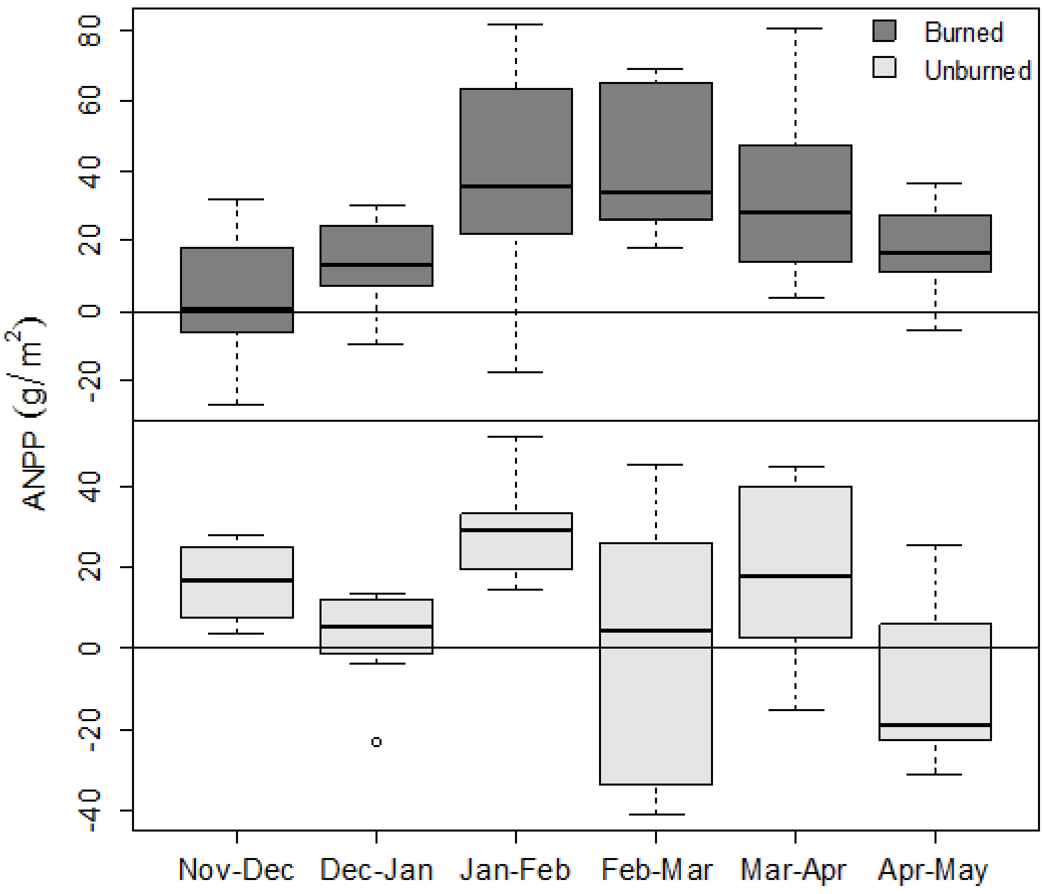

Figure 3.7: Monthly ANPP at the annually burnt site with heavy grazing and the unburnt site with light grazing over six months (November 2015- May 2016).

3.8 Discussion

3.8.1 Grazer presence on the firebreak

The camera trap method showed clearly a significant difference in grazer biomass between the two sites, the firebreak having relatively more grazer utilization. This agrees with the first hypothesis of this chapter which stated that the firebreak was going to have more grazer presence relative to the adjacent unburnt control, due to short and nutritious grass growing on the firebreaks. Despite this, the dung counts showed no significant difference in grazer presence between the firebreak and the adjacent unburnt control. Using dung counts has been criticised due to the fact that it does not take into account for the contamination by animals dropping their dung at the site while on their way to graze somewhere else and also not accounting for dung beetle activity (Barnes *et al.* 2010), and our comparison between treatments might also have been confounded by faster decomposition rates on the firebreak plots where there was lower vegetation cover. For this reason I find the camera trap data more reliable as they are a true measure of grazer presence on each treatment.

Another interesting finding of this study was that from the overall selectivity index, all five of the common grazers (red hartebeest, blesbok, impala, wildebeest, zebra and gemsbok) at the site had a strong selectivity for the firebreak relative the unburnt control. The wildebeest and the hartebeest had the highest selectivity which corresponds with the findings on the previous chapter (Chapter 2) where these two had the strongest affinity to grazing on shorter grass height of less than 10cm. Such grass height only existed on the firebreaks.

Analogous to these findings, in the USA, Allred *et al.* (2011) found that ungulates preferred grazing on recently burnt areas and avoided areas with long time since fire in Tallgrass prairie. They further found that forage quality was inversely proportional to long-time since fire; hence the ungulates were attracted to the recently burnt areas to graze on fresh high quality short grass. Many previous studies in African ecosystems have also demonstrated a short-term response to fire where grazers are attracted to the post-fire regrowth (Wilsey 1996; Tomor and Owen-Smith 2002; Sensenig *et al.* 2010). However, here I have shown that this attraction continues even after many years (10+) of repeated burning and grazing. Burkepile *et al.* (2013) also demonstrated this in a long term experiment in the Kruger National Park – although in their study only the wildebeest showed a consistent preference for the frequently burned and grazed plots. Therefore the firebreaks represent a grazing resource and could be considered beneficial at a landscape scale.

3.8.2 Herbaceous species composition

As expected I found a difference in species composition between the firebreak and the unburnt matrix. The firebreak had a higher Shannon diversity index. This could be an indication that these firebreaks are overgrazed to the point of reducing diversity. According to the theoretical models presented by (Milchunas *et al.* 1988) and also seen in Collins and Barber (1986), that greater plant diversity can be achieved under moderate grazing than under heavily grazed or ungrazed conditions. The importance of this combined effect of fire and grazing in promoting grass diversity, species richness and heterogeneity is further highlighted by many of the previous studies which showed that fire alone promoted homogeneity by reducing; species diversity, richness and community heterogeneity (Collins 1992; Hobbs 1996; Archibald *et al.* 2005; Collins and Smith 2006; Veen *et al.* 2008; Waldram *et al.* 2008; Cromsigt *et al.* 2009; Augustine and Derner 2014). On the other hand Augustine and Frank (2011) showed that grazing enhanced plant diversity by increasing resource availability and modifying the grass community structure and the species composition. When Collins and Smith (2006) coupled fire with grazing in their study in Tallgrass praire in the USA, they found that grazing on frequently burnt (annual burns) small patches significantly increased the plant community heterogeneity but decreased heterogeneity in infrequently burnt areas. Therefore, it is interesting to see that coupling fire with grazing in a nutrient poor and high rainfall Southern African Sourveld grassland (my study) also showed greater benefits for management purposes.

Some species at the site were unique to each treatment and the canonical correspondence analysis indicated a clear separation between the firebreak species and the unburnt control species, even though there are some species which could persist in both environments. In support of these findings, O'Connor *et al.* (2004) also found a clear distinction in species composition between the firebreaks and the adjacent unburnt grassland in a similar study in a Highland Sourveld in the Drakensburg. In my study, the grass species which were predominantly found on the firebreak are able to coexist with both frequent burning and heavy grazing. The fact that several sensitive (decreaser) species like *Themeda triandra* and *Heteropogon contortus* were still present on the firebreak indicates that the site is resilient to the level of grazing. Angassa (2014) observed a decline in *Heteropogon contortus* with an increase in grazing intensity, in a study done in the communal rangelands of Borana in southern Ethiopian. *Cynodon dactylon* also dominated the firebreaks gaining its tolerance from being both a stoloniferous as well as a rhizomatous grass (Veenendaal *et al.* 1996).

Even though frequent burning of South African mesic grasslands result in a grass community dominated by short to medium perennial grasses such as *Heteropogon* contortus and *Themeda triandra* (Belsky 1992; Archibald and Bond 2004), this study showed that if you couple fire with heavy grazing the dominance of these palatable species becomes intermediate due to the grazing pressure. As a result, some unpalatable species which resisted being grazed (by adopting the avoidance strategy) such as *Aristida* species (Briske 1996; Angassa 2014), eventually dominated. This switch in species composition or abundance from a palatable landscape to a less palatable landscape due to high intensity grazing (Snyman and Du Preez 2005; Angassa 2014) is also an indication of low landscape function (Snyman and Du Preez 2005). However, the significance of this unpalatability may be overshadowed by the fact that the firebreak still retains other palatable species that have gained more tolerance to constant defoliation by both fire and grazing. Moreover, the fact that most grass species remain palatable at shorter growth (O'Connor *et al.* 2004), also surpasses this effect of a switch in species composition on the firebreaks. Furthermore, a veld assessment conducted by Everson and Tainton (1984) on the Highland Sourveld of Natal showed the veld condition scores were significantly higher in grassland plots experiencing 30 years of annual burns and grazing relative to unburnt plots.

3.8.3 The functioning of the firebreaks

As expected I found that the firebreak had more signs of degradation in terms of percentage bareground, soil compaction, infiltration rates, but not soil moisture. These data were collected in December 2015, so are not simply a short-term response to the fire in April. This suggests that frequent burning coupled with heavy grazing can be detrimental to soil structure, and consequently be prone to continued poor landscape functioning and reduced productivity. These indicators are largely a result of the reduced aerial biomass on this site: soon after a fire event the green flush is intensively utilised by grazers, keeping the ground exposed throughout the winter and summer months. This exposure of bare ground increases the chances of soil erosion (Yong-Zhong *et al.* 2005) which further degrades the landscape. However, at this site I did not see any obvious signs of soil erosion. Moreover, high soil compaction on the firebreak as a result of the trampling effect by herbivores also increases bareground by hindering seed germination and seedling establishment (Veenendaal *et al.* 1996). The compacted ground prevents water from entering the soil column, and increases soil erosion. The increased bareground exposes the water in the surface soil to evaporation, so one would expect lower soil moisture on the firebreaks. Although my soil moisture measurements were lower, they were not significantly so. This could be because I did not have enough replicates to demonstrate the pattern. Alternatively, soil moisture can increase in systems with less vegetation cover because transpiration losses are less (Zhou *et al.* 2007). Soil moisture is a complex outcome of many variables and more detailed data would need to be collected to test the alternative hypotheses at my site.

Other studies on grazing impacts have documented similar results, that with an increase in bareground together with the trampling effect by herbivores (Martínez and Zinck 2004) tend to increase the compaction of the soil (Pietola *et al.* 2005) which results in low infiltration rates and ultimately low soil moisture (Snyman and Du Preez 2005) as well as high surface runoff resulting in high soil erosion (Horn *et al.* 1995; Snyman 2003; Martínez and Zinck 2004; Pietola *et al.* 2005; Snyman and Du Preez 2005). Moreover, O'Connor *et al.* (2004), working on a firebreak in the Drakensberg, found that the firebreaks were lower in both carbon and nitrogen content and had more acidic soil. They did not find differences in infiltration rate however. However, (Savadogo *et al.* (2007) in relation to this study, also found a lower infiltration rate on frequently burnt plots than on unburnt plots in Burkina Faso. Furthermore, another study done by Rice and Parenti (1978) in a tall-grass prairie in Oklahoma, showed that the soil moisture content was lower in mowed and burnt plots relative to the controls.

3.8.4 Grass Annual Net Primary Productivity (ANPP)

Unexpectedly the annual ANPP on the firebreak was higher (146.42g/m^2) than that recorded on the unburnt control (56.47g/m^2) which refuted the third hypothesis which stated that there was going to be a lower productivity on the firebreaks. These values were still low (especially the unburnt control) relative to what has been recorded in the literature in similar studies receiving similar rainfall. According to Scholes (1990), unfertile high rainfall sourveld grasslands should at least yield about 150g/m^2 of herbaceous production at 700mm of rainfall per annum. Even though my study site generally receives high annual rainfall of above 650mm (Figure 1.2), lower herbaceous production recorded could have been due to a delay in rainfall season as the year 2015 only received a total of 445mm of rainfall and the rains only arrived late in January 2016, hence the lowest ANPP was recorded during the months of November and December 2015 (Figure 3.7). In another similar study done by Everson and Everson (2016) on a montane or Highland grassland of the KwaZulu-Natal Drakensberg, they also found that the productivity was higher (144.7-154.5g/m^2) on the regularly burnt and grazed grassland relative to the unburnt (118.2g/m^2). This grassland also received high annual rainfalls of about 1300mm and the burnt plots experienced a long term effect of fire and consequently increased grazing (the plots were 25 x 25m in size) for over 30 years of annual burns (Everson and Everson 2016).

It has often been shown that sites recovering from fire are more productive than unburned vegetation(Abrams *et al.* 1986; Briggs and Knapp 1995), but the fact that this site – which has been heavily utilised by grazers for at least 10 years and by all indices appears very poor in landscape functioning - has higher ANPP forces us to rethink our assumptions about degradation in grasslands. The firebreaks could have been less heavily utilised than they appeared (based on having high plant diversity), the following reasons can further validate this. The fact that firebreaks are burnt early in the dry season whereas the rest of the burns within the farm takes place later during spring, creates an ecological mosaic within the landscape such that grazers get to move around the farm following recently burnt areas (O'Connor *et al*. 2004). The movement from the firebreaks to the newly burnt areas allows the firebreaks to be rested therefore hindering overgrazing (O'Connor *et al.* 2004), i.e. although the firebreaks act like small fires, there are also large fires most years in the rest of the landscape, and the overall outcome is grazer dilution/dispersal. During our study year there were few fires (neighbouring burn and other firebreaks burnt later during the year) in the reserve even though it was a drought year. So it appeared that animals could have moved around to other burnt patches, resting the firebreak, and this could be a strong explanation as to why the firebreaks at the studied site remained more productive under the pressure of both fire and grazing.

Explanations for why the unburnt area had lower productivity relate to the specifics of grass growth form. Veen *et al.* (2008) found that grazing enhanced light and nitrogen availability. Moreover, Hulbert (1986) also found that the removal of dead plant material by fire or clipping resulted in more rapid growth, and that the increased light for new growth through the removal of dead material seemed to be highly important in many studies he reviewed. Therefore, what could explain the lower ANPP on the unburnt site is the fact that growth in tall Sourveld grasslands with high accumulation of moribund is notoriously suppressed because light cannot penetrate to the growth tips of the grass (Hulbert 1986; Knapp and Seastedt 1986; Masubelele 2007; Veen *et al.* 2008). In contrast, grass on the firebreaks is kept at short heights in most of the time during the year due to constant defoliation by fire followed by grazing. This allows the sunlight to penetrate very easily to the grass, and subsequently result in higher productivity relative to the unburnt control. Moreover, the adjacent unburnt site had tall grasses shading shorter grasses from receiving the sunlight. Therefore, the above assumes that the cost of having photosynthetic tissue removed is less than the benefit of increased light availability. Another justifiable theory which links with light competition mentioned above is the “grazing optimization hypothesis”. This hypothesis predicts more productivity or biomass on grazed plant communities than ungrazed ones through compensation for effects of defoliation (Hobbs 1996). Therefore, the “grazing optimization hypothesis” can be an explanation as to why the firebreaks had a high Aboveground Net Primary Productivity, and this hypothesis has been proven in various studies done in several ecosystems (McNaughton 1979; McNaughton 1983; Hobbs 1996)

Other explanations for increased productivity in tall-grass prairie systems relate to the higher soil temperature (due to the absence of the insulation effect of litter) in the burnt and mowed plots early in the growing season (Rice and Parenti 1978). This is unlikely to be the reason at my sites, which are not similarly temperature limited.

3.9 Conclusions

In conclusion, the firebreak was clearly selected by grazers over the adjacent unburnt matrix. Even though this resulted in several signs of degradation, these firebreaks still remained more productive and diverse and at the same time benefited grazers with fresh and palatable green flush after the fire than the unburnt (and lightly grazed) landscape. This could be an indication that these firebreaks are not as heavily utilized and/or overgrazed as I initially thought. Moreover, the species composition on the firebreak suggested an increase in the occurrence of species that are tolerant to both grazing and fire, but did not indicate particularly intense grazing as some sensitive species (decreasers) were still there. So: moderate to heavy grazing resulting from small fires is not necessarily destructive of primary productivity and can even aid secondary productivity and increase biodiversity. Firebreaks are an essential fire management tool and any impacts on grazing, ANPP, or biodiversity are secondary, but perhaps repeated small fires are something that managers could consider to increase the diversity, resilience and productivity of their rangelands. It is also imperative to think about spatial aspects in managing such systems, such that the size of the firebreaks should not be too big to disperse the animals or too small to be overwhelmed with overgrazing.

4 Chapter 4:FINAL DISCUSSION & CONCLUSION

The maintenance of heterogeneity in Highveld grasslands characterised by tall unpalatable grasslands could be a positive management tool in these ecosystems. This study showed that structural heterogeneity could be maintained in these grasslands through implementing small fires, therefore concentrating grazers in those small patches. By so doing, the grass can remain short in those patches, therefore, remaining palatable as it has been documented that as long as the grass stays short it stays palatable (Sensenig *et al*. 2010; Arsenault and Owen-Smith 2011) i.e. even in a high-productivity site grazers can maintain short-grass patches or grazing lawns once they have been created by fire. The fact that the grass at the investigated firebreaks (>10years of annual burns) remained attractive to the herbivores is an indication that this structural heterogeneity can be maintained over time. This study indicated that the size of the burn and the type of grazer species are among the key factors in maintaining these high forage quality grazing lawns or "hotspots". For, instance the short grass specialists such as wildebeest, blesbok and gemsbok proved to be responsible for keeping the grass short (below 10cm) throughout the study period. This finding is very important as these are some of the most common grazer species found in Highveld grasslands and they accounted for about 40% of herbivore biomass at the study site. The presence of short-grass specialists in this ecosystem is an indication that these short-grass patches must always have been a part of the Highveld grasslands, and the high diversity and resilience of the patches I studied also suggest that this type of disturbance is intrinsic to the system. Moreover, a 5ha burn and the firebreaks proved to be small enough to concentrate grazers on one spot, but ideally one should test the impacts of different fire sizes over several years to establish the appropriate fire size for the landscape in the long run.

A common way of using fire to manage rangelands and conservation areas in the Highveld is to burn different sections each year – creating a shifting mosaic of short attractive green grass, which is aligned with rotational grazing paradigm which aims to prevent heavy grazing in any one part of the landscape through moving animals between camps (Tainton 1972; Winter *et al.* 2012). The shifting mosaic also creates short-grass patches for the short-grass specialists, but this research (and previous studies e.g. Wilsey 1996) show that this habitat is likely to last only a short period of time after the rains come. However, the management strategy

I have been investigating is the exact opposite: burning the same patch of land every year (on the firebreaks) to initiate and create heavily grazed and utilised patches. Moreover, the small fire (5ha) we implemented maintained short-grass areas until the end of the growing season in this study, of-which extrapolating that to several years of small annual burns and grazing on the firebreak also showed that these short grass patches can be maintained over years.

Furthermore, these different management strategies also have different consequences on grass diversity. The main aim of the shifting mosaic approach is to maintain the species composition of these grasslands, and will not result in novel grass communities. In my study repeated fire and grazing on the same small area (firebreak) proved to positively affect the grass community by increasing grass diversity. Another critical thing to consider when implementing these management tools is the impact on other flora and fauna. Even though my study did not investigate the impact of creating and maintaining short-grass grazing patches on other flora (e.g. forbs) and fauna (such as birds and invertebrates) occurring at the site, however, my colleague, Maggie Parish who worked on forbs at the site as well for her Masters project, found that the forb community was not changed by these disturbances (Maggie Parish MSc Thesis 2017) perhaps due to the fact that most of the herbivores at the site were strictly grazers with the exception of just a few which are mixed-fed (impala) or browsed (deer and kudu). However, there is substantial literature from other ecosystems indicating a specialist short-grass flora of insects and birds which would be promoted by this type of management (see detailed literature review of this in Chapter 2), hence the increase in diversity. All in all I suggest there are enough benefits to this type of fire management practice to propose initiating it in conservation areas in the Highveld. Whether it is appropriate for cattle farming is something that needs to be considered separately – as cattle are not considered short-grass specialists and might respond differently.

Clearly there is no “one size fits all” when it comes to maintaining different rangelands – it really depends on the type of rangeland one is managing. For instance the shifting mosaic approach might be more appropriate in the Lowveld (Sweetveld) if the landscape is more uniformly palatable (spatially and throughout the year), than in Highveld grasslands (sourveld).

There are two conceptual models which are relevant to my research. Hempson (2004) proposes that the probability of establishing and maintaining grazing lawns will increase when forage quality is generally low, and will depend on the rainfall and grazer densities at a site. This was supported by my data. Moreover, Milchunas (1998) suggests that at high rainfall systems with an evolutionary history of grazing biodiversity will show a positive response to increased levels of grazing intensity (up to a point), and this is also confirmed by my data.

Finally, another important consideration on these different management tools is the feasibility of implementing them – i.e. how easy it is to implement them. Block burns are easy to implement as one can use roads and natural firebreaks to control the area burned. Smaller, more contained fires and firebreaks take more time and human resources. However, there are advances in techniques for initiating open-ended firebreaks which make use of the range of weather conditions during the day and carefully control the timing of fires. These could be explored as a way to ease the implementation of small fires. Moreover, if the grazers are effective enough in keeping the grass short repeated burns could be infrequent therefore reducing the costs of implementing the burns now and again.

There were some unforeseen circumstances and technical issues that affected this study. For instance, the camera data was somehow affected by cameras suddenly stopping working due to batteries running low and cameras being moved out of position by the herbivores et cetera. Luckily, we were able to define analysis methods which were not affected by this. Moreover, the soil moisture could have probably yielded similar results to other classic degradation parameters if adequate replicates were collected. Lastly, the drought on the year I started the experiment mean that although I showed that the treatment kept the grass short I was not able to conclude whether this would have been the case in a year with more representative rainfall.

Therefore, for future studies, more regularity on checking cameras needs to be taken into consideration. Cameras can also be mounted firmly to avoid movements, however in my case I had to deal with the trade-off between mounting cameras on bigger shrubs (that were mostly more than hundred meters away from the site) and smaller shrubs which were at appropriate view (less than 10m) to the site. Moreover, I could not use some poles to mount the cameras on as I wanted to minimise theft of those cameras since the site was open to public – so I had to hide them on those shrubs. I could also have directly assessed soil degradation by trying to quantify soil erosion.

Something that I did not do, but that would have aided my interpretation of my results is to quantify grass productivity on a newly burnt site and compare with the results I presented for a repeatedly burned and grazed site and an unburned site. It is likely that immediately post-fire the productivity of the tall grassland will be higher than both the unburned grassland and the frequently grazed one, as it will be re-growing in a high light and nutrient-rich environment after being well rested from grazing. The mean grazer density at the site was around 2000kg/km^2 and at my experimental burns the density calculated from camera trap data ranged between 5000 and 1500kg/km^2 over the study period (Figure 2.4 in Chapter 2). By assuming an average grazer mass of 180kg (weighted mean of all grazers at the site) and an energy concentration of 6MJ/kg for the grass it is possible to use Equation 1 (from Dong *et al*. 2006) to determine how much grass these grazers were eating.

$$\text{DMI} = \text{SBM}^{0.75} \text{ x } \frac{(0.0119 \text{ x } \text{NE}^2\text{ma} + 0.1938)}{\text{NEma}}, \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\text{Equation 1}$$

where; DMI (which is the dry matter intake) is measured in Kg/head/day, SBM is the live body weight in kg and NEma is the energy concentration of the diet in in MJ kg^{-1} (Fox *et al.* 2004; Dong *et al.* 2006; Archibald *et al.* 2016). I calculate that the densities of grazers measured on my sites with the camera traps could have resulted in from 15 to 51g/m^2 of herbivore offtake over the entire year, which is a significant proportion of the productivity that I measured on the other two sites.

Lastly, in terms of rainfall, it would take more years of data and a range of fire sizes and grazer densities to determine the effectiveness of this fire application in creating and maintaining short grass ecosystems in the Highveld, even though this study has for the first time demonstrated the possibility that such systems can be created and maintained.

In closing, my personal highlights of the study among others were; i) for the first time, finding that short-grass grazing lawns can be created and maintained in the high rainfall nutrient poor Highveld grasslands, ii) that the grazer species such as wildebeest, blesbok and gemsbok were the key short-grass specialists in the maintenance of those grazing hot-spots, iii) being puzzled and simultaneously fascinated by the firebreaks initially thought to be poor in landscape function turning out to be highly productive and finally, iv) this study adding a new perspective to managing rangeland or grassland ecosystems.

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