

**Fire history and frost in a semi-arid savanna woodland:
Understanding their impacts on vegetation structure and species
composition in the Waterberg Plateau Park, central Namibia**

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ABSTRACT

Fires are inevitable in savanna ecosystems and play a major role in shaping vegetation structure. Generally, an increasing fire frequency favours the grass component, while the woody plants remain in the fire trap. Conversely, a reduction in fire frequency is believed to be one of the contributing factors for bush encroachment and decreased perennial grasses. Thus, fire cannot be disregarded when considering the management of rangelands for both domestic livestock and wildlife. A disturbance that is rarely studied and may be important to understand is frost occurrence in savannas. In the study area it occurs frequently, particularly in low-lying areas (interdunes) during winter when temperatures reach freezing point. Since there is very little information on how frost affects vegetation dynamics in southern African savannas, results from this study may provide some insight. The study was conducted at the Waterberg Plateau Park, a semi-arid savanna woodland considered the south-western limit of the "Tree savanna and Woodland" zone. The park experiences a range of fire frequencies, from both natural and anthropogenic causes, and its fire history is relatively well-known. The study broadens our knowledge and fills a gap especially in Namibian savanna woodlands at the arid end of the scale. The main aim of the study was to understand how fire history and frost occurrence affect vegetation structure and species composition.

Four blocks with different fire histories: fire treatments burned 1 year, 2 years, 14 years and 24 years ago at the time of data collection and with mean fire return interval of 6.2 years, 9.3 years, 9.3 years, and 18.5 years respectively were surveyed. Fire treatments will be referred to by the number of years since last burn as follows: Treatment 1, Treatment 2, Treatment 14 and Treatment 24. The frost study was conducted in an area with a clear dune-interdune effect and that was last burnt 24 years ago, with a mean fire return interval of 12.3 years. Three sampling methods were used: the adapted point-centred quarter (PCQ) method to determine vegetation structure and species composition, the Bitterlich gauge to estimate woody canopy cover, structure and species composition and the visual obstruction reading (Robel pole) method to estimate grass biomass. For the frost study, in addition to these measures, soil samples were collected and analysed and the winter temperatures recorded.

The study showed that recent fires resulted in higher perennial grass density ($P < 0.05$) with higher relative density of good grazing value grass species ($P < 0.05$), but significantly lower grass biomass ($P < 0.05$). This is because fire stimulates the recruitment and regrowth of new grass shoots through removal of moribund grass, litter and reduces competition between established plants. The lower grass biomass recorded in the recently burned area was partially due to the highly nutritious post-fire regrowth that is attractive to grazers, thus reducing the biomass. This reduced grazing pressure in other areas allowing for significant

biomass recovery, such that 2 had significantly ($P < 0.05$) higher grass biomass. Fire also changed the grass species composition towards more palatable grasses, while reducing the unpalatable grasses.

Fire did not significantly ($P > 0.05$) affect overall woody density but the density of woody plants in different height classes was significantly different ($P < 0.05$). Treatment 2 had higher woody density than treatment 24 in the < 1 m height class. Treatment 1 had lower woody density in the 1 m-2 m height class than all treatments, while in the 2 m-3 m and 3 m-4 m height classes treatment 24 had higher woody density. Interestingly, treatment 1 and treatment 14 had higher woody density in the > 4 m height class. As overall woody density was not different suggests that very little total mortality occurred but only stem mortality occurred, probably due to fires being of low intensity as a result of low grass biomass (highest being 1425 Kg/ ha). In contrast, overall woody cover significantly increased ($P < 0.05$) with time since last burn and woody cover in the different height classes also differed significantly ($P < 0.05$). Woody plants in recently burned areas are top-killed, resulting in a more open woodland savanna, dominated by woody plants < 2 m that contribute to woody cover. Increases in canopy cover with time since last burn is thus shown to be merely increases in the cover of individuals and not as an increase in the number of individuals. The dominating woody species found in all the surveyed treatments was *Terminalia sericea*, a species that is fire resistant as it coppices vigorously when damaged and is considered an encroaching species in the study area. Woody species composition in this savanna woodland like other semi-arid savannas is mainly influenced by soil nutrients and not fire.

The frost study showed that the interdune areas had significantly ($P < 0.05$) lower average temperatures of -3.87 °C, average minimum temperatures of -14.3 °C and higher number of days (89) with temperatures ≤ 0 °C as well as the lowest temperature recorded of -14.6 °C than the dune areas with -3.02 °C, -10.5 °C, 80 days and -13.6 °C respectively. This is because cold air settles in the interdunes as an influence of topography. The dune areas also experienced surprisingly low temperatures. The interdune areas had higher perennial grass density ($P < 0.05$) which was mainly of good grazing value species. This could be an indirect result of frost as it top-kills woody plants and allows more light penetration to the grass layer, thus also influencing grass species composition towards good forage species. The grass biomass between the interdune areas and dune areas did not differ and was quite low (652.7 kg/ ha and 557.9 kg/ ha respectively).

The overall woody density did not significantly differ ($P > 0.05$) but only differed in the > 4 m height class ($P < 0.05$), with the dune areas having higher woody density than the interdune areas in the aforementioned height class. In contrast, total woody cover was significantly

higher ($P < 0.05$) in the dune areas (54.2%) than the interdune areas (40.8%). The interdune areas had significantly ($P < 0.05$) higher woody cover of the < 2 m woody plants and lower of the > 3 m woody plants and vice versa for the dune areas. Like fire, frost appears to only cause mortality of above-ground biomass (top-kill) with resprouting occurring when conditions become favourable in the growing season. Annual frost events therefore confine woody plants to shorter height classes in what could be termed as a “freeze trap”. Woody plants growing in the dune areas tend to grow unhindered to > 4 m height classes and probably become more frost resistant with an increase in stem diameter. The results also show that *Terminalia sericea* is frost-tolerant as it was the dominant species in the interdune areas. *Acacia ataxacantha* and *Ochna pulchra* on the other hand, contributed significantly lower relative woody cover in the interdune areas than in the dune areas, suggesting that they are less tolerant to frequent frost events.

Fire positively affected the grass component by increasing grass density, enhancing productivity through removal of moribund material and plant cover, but, grass biomass was significantly reduced. However, fire did not significantly alter woody species composition. Savanna vegetation is well adapted to fire and woody plants may persist as gullivers. Therefore, fire maintains an open savanna through top-kill by reducing woody plants to browsable heights. Frost seems to indirectly affect grasses through increased light penetration as it causes above-ground mortality of woody plants. Like fire, frost mostly top-kills woody plants confining them to shorter height classes (in a freeze trap) thus reducing canopy cover, but does not significantly reduce overall density. Frost is also an important limiting disturbance that influences woody species composition by favouring more frost tolerant species such as *Terminalia sericea* in the study area.

Key words: fire history, savanna woodland, vegetation structure, species composition, time since last burn, frost, dune, interdune, Waterberg Plateau Park

DEDICATION

This thesis is dedicated to my wonderful mother Leena Frans, for her support, encouragement and all the sacrifices she has made for me and my siblings to have the best education and thus a better future. Thank you for always being there for us and giving us the best that you could offer. I sincerely appreciate everything you have done in my life and for being strong for us. You have done a great job with us mother.

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DECLARATION

This is a thesis prepared in partial fulfilment of the requirements for the Master degree in Natural Resources Management of Namibia University of Science and Technology. I, Vistorina Amputu, hereby declare that this study is a true reflection of my own research, and all literature used that does not belong to me is cited and referenced to acknowledge the appropriate author(s), and that this thesis, or part thereof has not been submitted for a degree elsewhere.

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Date:

ACRONYMS

E	East
GPS	Global positioning system
HCA	Hierarchical cluster analysis
KNP	Kruger National Park
LSD	Least significant difference
MET	Ministry of Environment and Tourism
N	North
NMS	Non-metric multidimensional scaling
NUST	Namibia University of Science and Technology
PCQ	Point-centred quarter
S	South
SASSCAL	Southern African Science Service Centre for Climate Change and Adaptive Land Management
SFT	Space for time
VOR	Visual obstruction reading
W	West
WPP	Waterberg Plateau Park

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Introduction

Savannas are peculiar ecosystems that are neither grassland nor forest, but characterised by the co-occurrence of two contrasting life forms that both contribute more or less equally to primary production (Scholes & Walker, 1993; Scholes & Archer, 1997; Wiegand, Saltz & Ward, 2006; Accatino, de Michele, Vezzoli, Donzelli, & Scholes, 2010; Trollope, van Wilgen, Trollope, Govender, & Potgieter, 2014). Savannas consist of a more or less continuous herbaceous component (mainly grasses) and a discontinuous woody component of shrubs and trees (Scholes & Walker, 1993; February & Higgins, 2010; Trollope et al., 2014). Thus, savannas are complex and diverse ecosystems rich in species, communities of plants, animals and habitats (Williams & Cook, 2001) and a thorough understanding of factors that structure savanna communities is required to guide their management (Zimmermann, 2009). The savanna biome occupies about 40% of Africa (van Wilgen, Biggs, Regan, & Mare, 2000), it is the largest biome in southern Africa, covering about 54% of its land (Cowling, Richardson & Pierce, 1997) and savannas cover 65% of Namibia (Okitsu, 2005). Generally, they are found in areas that receive rainfall between 200 and 1800 mm per year (Johnson & Tohill, 1985 in Zimmermann, 2009). They are important ecosystems used as rangelands mainly for livestock and wildlife, agriculture, and host some of the largest and famous conservation areas such as Etosha National Park, Kruger National Park, and Serengeti National Park. Therefore, savannas are fundamental to African livelihoods, providing ecosystem services ranging from economic resources to social, cultural and spiritual services (Scholes & Archer, 1997; O' Higgins, 2007; Khavhagali & Bond, 2008).

Attempts to answer what Sarmiento (1984) in Riginos (2009) terms as a "savanna problem" generally falls into two categories: Competition-based models mainly consider niche partitioning mechanisms by which trees and grasses avoid competition, usually for water (Riginos, 2009). Walter (1971) proposed that due to the separation of rooting niche, trees have sole access to water deeper in the soil as they have deeper roots and grasses are strong competitors for water in the surface horizon of soil and are thus able to coexist (Scholes & Walker, 1993; du Toit, Rogers, & Biggs, 2003). While demographic models invoke factors (rainfall, fire, herbivory and the interactions thereof) that limits vegetation growth and survival (Riginos, 2009). Higgins, Bond & Trollope (2000), hypothesized that the interaction between life history characteristics (sprouting ability, fire survival at different life stages and mortality) and fire occurrence which do not allow recruitment of trees into adult life classes

could explain this coexistence (du Toit et al., 2003). These models show factors that prevent the woody component from completely dominating, thus allowing it to coexist with the grass component.

1.1.1 Determinants of savanna ecosystems

The primary determinants of savanna ecosystems are moisture availability and soil nutrient status (bottom-up factors), while herbivory and fire (top-down factors) are the main secondary determinants (Scholes & Walker, 1993) but also includes other less considered factors such as frost. The interactions of these factors determine the structure and productivity of savannas.

Moisture availability is a key determinant that influences the distribution and productivity of vegetation in all biomes and is considered a critical driver of savanna structure (Sankaran et al., 2008). Savanna ecosystems are characterised by alternating hot wet and warm dry seasons (Scholes & Archer, 1997; Trollope, 2003; Williams & Cook, 2001). In southern Africa, they can be divided into an arid and moist group, (Huntley, 1982 in du Toit et al., 2003). In more humid savannas the tree-grass co-existence is considered to be mainly due to the occurrence of fire (without fire savannas would eventually be replaced by forests) (Bucini & Lambin, 2002; Cech, Kuster, Edwards, & Venterink, 2008). This type of savanna is prevented from becoming dominated by the woody component through the top-kill of saplings that are unable to escape the fire sensitive stage when fires are sufficiently frequent (Accatino et al., 2010; Joubert, Smit, & Hoffman, 2012). In drier climates, however, the equilibrium between woody and grass cover and productivity seems to be mainly determined by water availability (Cech et al., 2008), where grass primary production increases with increase in annual rainfall (Accatino et al., 2010) and increases the chances of fires (Govender, Trollope, van Wilgen., 2006). A slightly alternative viewpoint by Joubert et al. (2012) is that fire in more arid savannas although not as frequent, is just as important as in humid savannas as it limits woody plant recruitment by killing seedlings.

Soil nutrient availability, especially soil nitrogen, is another important determinant of savannas contributing to plant growth and production (Scholes & Walker, 1993). Soil nutrients are influenced by soil texture and moisture availability (Sankaran et al., 2008). Environmental factors such as moisture availability and sunlight that increase establishment and tree growth interact with soil nutrient status, increasing leaf growth and development of the root system (Scholes & Archer, 1997). Soil nutrients and texture determine the distribution of fine-leafed (clay-rich soils) and broad-leafed savannas (nutrient poor soils) (Scholes, Dowty, Caylor, Parsons, Frost & Shugart, 2002). Fine-leafed savannas indicate

ecosystems with palatable grasses, less frequent fires and are referred to as eutrophic or nutrient –rich savannas, while broad-leafed savannas indicate more frequent fires, with less palatable grasses and are referred to as dystrophic or nutrient poor savannas (Scholes & Walker, 1993; Scholes et al., 2002).

Fire, whether caused by lightning or human-induced, is an integral part of savannas and has influenced savannas over the course of their evolution (Williams & Cook, 2001). The main reason for using fire in savannas is to remove moribund and/ or undesirable grass material (Trollope, 2004; Bothma & du Toit, 2010) and to control and/ or prevent the encroachment of undesirable plants (Trollope, 2004). Humans have used fire for tens of thousands of years mainly for shifting agriculture, for increasing fresh growth of vegetation for livestock grazing, clearing land for agriculture, maintaining grasslands, controlling pests, and removing dry vegetation and crop remains to promote agricultural productivity (Bucini & Lambin, 2002; Trollope, 2003; Sheuyange, Oba, & Weladji, 2005). In north-eastern Namibia, fire frequencies have been increased to such an extent that some areas are burned annually for shifting agriculture (Joubert, Rothauge & Smit, 2008). However, especially on most commercial farms fire frequency has been reduced due to low fuel loads or because fires are deliberately excluded (Joubert et al., 2008). Rangeland managers in protected areas also use fire as a conservation management practice (Bucini & Lambin, 2002; Trollope et al., 2014). In Etosha National Park for example fire is used to reduce and prevent the occurrence of devastating fires that may spread extensively (M. Kasaona, personal communication at Etosha National Park, September, 2013). Anthropogenic fires account for over 70% of the yearly fires in African savannas (Sheuyange et al., 2005). The main effects of fire on woody vegetation, is that it causes mortality of seedlings (Joubert et al., 2012) and top-kills woody vegetation (Trollope, 2003), thereby maintaining open savannas, which in turn promotes grass growth (van Langevelde, van de Vijver, Kumar, van Koppel, de Ridder, van Andel, Skidmore, Hearne, Stroosnijder, Bond, Prins, & Rietkerk, 2003). Fire in combination with other factors affects vegetation structure and species composition, which in turn influence animal diversity, food availability and habitat diversity (Bothma & du Toit, 2010).

African savannas are home to most of the world's livestock and large wild herbivores (Scholes & Walker, 1993; Riginos, 2009), thus grazing and browsing particularly shape them. Herbivory and fire affect savannas through direct and indirect effects (van Langevelde et al., 2003) and both remove plant material. Fire and herbivory are direct competitors for plant biomass (van Langevelde et al., 2003; Gul, Islam, Ahmad & Gul, 2014), and their interaction influences vegetation composition, annual aboveground net primary productivity and nutrient cycling (Archibald, Bond, Stock & Fairbanks, 2005). Like fire, browsing herbivores reduce

woody vegetation and may reduce trees to smaller size classes (flame zone) making them more vulnerable to impacts of fire (van Langevelde et al., 2003). Grazing herbivores remove grass biomass, reducing fuel loads which make fire less intense, or may even prevent fires altogether (du Toit et al., 2003; van Langevelde et al., 2003; Archibald et al., 2005). Utilisation of vegetation by herbivores before and after burning may significantly change the composition and structure of vegetation (Trollope, 2003). Herbivory after disturbances such as fire may limit the recovery of vegetation, while at the same time maintaining ecosystem structure or altering it (Shackleton, 1997 in Moyo, 2013). An example of how herbivory can alter the structure of savannas, is intensive grazing (overgrazing) that weakens grasses eventually leading to their removal, allowing woody plants to establish and lead to bush encroachment (Scholes & Archer, 1997). Herbivores also influence nutrient cycling through urine, trampling and dung droppings (Shackleton, 1997 in Moyo, 2013).

One factor that distinguishes African savannas from other fire-prone areas such as Australia and America is the presence of mega herbivores (du Toit et al., 2003). They are considered to have a major controlling influence on tree-shrub-grass balance. The most profound and well-known case is the effect of elephants on vegetation (van Langevelde et al., 2003; Holdo, 2005). Several studies (Mapaure & Campbell, 2002; Trollope, 2003; Mapaure & Moe, 2009) have looked at how elephants, sometimes in conjunction with fire (Holdo, 2005; Holdo, 2006) have altered vegetation structure by reducing tree height and density and thus opening up closed woodlands and in some areas even converting woodlands to grasslands (Holdo, 2006). Elephant-induced damage to woody plants makes them more prone to impacts by fire and frost, especially trees in smaller size classes (Holdo, 2006). For example, removal of bark through elephant browsing may expose vascular cambium of stems to freezing temperatures, intensifying the subsequent effects of frost or fire (Holdo, 2006). Although the study area does not have elephants it has both black and white rhinos which may be having a similar effect on woody plants, especially the black rhino as it is a browser.

Frost is another disturbance that occurs in the savanna biome (Mendelsohn & el Obeid, 2005; Whitecross, Archibald & Witkowski, 2012), during extreme cold winter periods. Frost causes the drying of above-ground plant tissues resulting in the top-kill and resprouting of woody plants (Holdo, 2005). Frost occurrence in an area may also inhibit the growth and establishment of frost-sensitive plants. Frost is often overlooked when compared with more noticeable disturbances such as fire and herbivory, and thus there is scarce literature available. Very little research has been done on the effects of frost on vegetation within savanna systems, (Holdo, 2005; Holdo, 2006; Whitecross et al., 2012; Henschel, Muller & O'Connor, 2016).

Therefore, climatic variability, soil dynamics, fire, large herbivores and other factors that are not often considered such as frost occurrence interact to shape African savanna vegetation, driving spatial and temporal heterogeneity across landscapes (du Toit, et al., 2003).

1.2 Background and problem statement

The Waterberg Plateau Park (WPP) was divided into five farms in 1956 and utilised as a grazing area for cattle until 1972 (Schneider, 1993). Farm owners burned about every 3-4 years depending on whether it was a wet or dry year (Jankowitz, 1983). During 1958 the entire park burned from a lightning induced fire. Thereafter, no major fires occurred until 1977, when another lightning fire burned about 20 000 ha (Jankowitz, 1983). The farms were purchased by the then Department of Nature Conservation in 1972 and the 41 000 ha land declared as a nature reserve (Schneider, 1993). A controlled fire policy was implemented and no artificial fires were allowed, and when a fire occurred it was only allowed to burn in the block it started (Jankowitz, 1983). Reduced fire frequency might have led to the thickening up of the woody strata (example *Terminalia sericea*) and the reduction in density of palatable climax perennial grass species such as *Anthephora pubescens*, *Brachiaria nigropedata* and *Digitaria seriata*. Coarse sour grasses such as *Eragrostis pallens* now dominate the plateau (Jankowitz, 1983).

Fires on the plateau are mainly accidental or planned as well as a few caused by lightning (Jankowitz, 1983). The WPP is divided into six fire management zones, which are further divided into two or three equal fire blocks. The main fire zones have different mean fire return intervals which range from every 6.2 years to 18.3 years (Joubert, unpublished data). The relatively well-known fire history of the park provided an opportunity for the investigation of how fire history affects vegetation structure and species composition.

In some parts of the WPP there is a fairly well established dune (higher elevation) system with interdunes (low-lying areas). Frost occurs during winter when temperatures drop below 0 °C, but likely more frequent and severe in the interdunes. As indicated earlier, very few studies have been done on how frost affects vegetation dynamics in southern African savannas, therefore frost effects were investigated to understand and provide insight on how it influences vegetation structure and species composition.

The significance of the study most importantly leads to a better understanding of a savanna woodland on dystrophic sandy soils, with regard to how fire history and frost occurrence alters vegetation structure (density, cover, grass biomass and grazing value of perennial grass species) and species composition. The WPP is also considered to be the southwestern limit of the “Tree savanna and Woodland” zone (Craven & Marais, 1989; Schneider,

1993) which lacks knowledge on how fire affects vegetation structure and composition. In a broader sense the study will contribute mainly to a better understanding of fire ecology in savannas, more particularly to savanna woodlands at the arid end of the scale, as fire is seldom researched in Namibia and remains a controversial issue. Therefore, the findings are not restricted to the WPP as findings may be useful and provide insight on understanding other similar savanna woodlands. Secondly, the study also provides insights on how frost affects vegetation structure and species composition and can be a building block towards understanding this disturbance in savannas. The improved understanding of fire ecology from this study could also assist WPP management in determining appropriate fire management practices for the park.

1.3 Overall aim, hypothesis and research question of the study

The overall aim of the study was to understand how fire history and frost affect vegetation structure and species composition in a semi-arid savanna woodland. The study sought to address the following research question: How do fire history and frost affect vegetation structure and species composition in a semi-arid savanna woodland?

The study is part of a broader project funded by SASSCAL investigating the effects of fire history on ecosystem processes and biodiversity in a semi-arid savanna woodland. Examples of the various research components are root carbohydrates, soil dynamics, animal utilisation, animal movements and various invertebrate species such as beetles, ants, wasps and bees. All these projects are being done on the same transects in the different fire treatments.

1.4 Structure of the thesis

The thesis is composed of five chapters, the first of which covers a general introduction of what savannas are and their key determinants, the background to the study and problem statement as well as the overall aim, hypothesis and research question of the study.

Chapter two describes the study area in detail, including where it is located, its extent, geology, climate, flora and fauna found there.

Chapter three is self-contained and addresses how fire history affects vegetation structure and species composition in a semi-arid savanna woodland. The chapter starts with an introduction of fire occurrence in savanna ecosystems and how it affects vegetation. This is followed by a literature review describing fire regimes and how fire affects vegetation in African savannas. Then, the specific objectives, research questions and hypotheses are outlined. The methods used for data collection and data analysis to address the research

questions are described, followed by the findings and the discussions thereof. The chapter ends with conclusions drawn from the findings.

Chapter four follows the same outline as that of chapter three, but addresses the objective of how frost affects vegetation structure and species composition in a semi-arid savanna woodland.

This thesis concludes with chapter five, which consists of conclusions from the study and recommendations drawn from the findings. It is hoped that the WPP management, conservation scientist and academics will benefit from some of the findings and insights presented in this thesis.

The nomenclature used in this thesis is the one used by the National Herbarium (WIND) as detailed in Klaassen & Kwembeya (2013), which is the latest Namibian plant species list published.

CHAPTER 2

DESCRIPTION OF STUDY AREA AND OUTLINE OF VEGETATION SURVEYS

2.1 Study area

2.1.1 Location and extent

The Waterberg Plateau Park (WPP) is a national park found in central Namibia, about 280 km northeast of Windhoek and about 60 km east of Otjiwarongo (Schneider, 1993) as shown in figure 1. It is situated at S 20.3971° and E 17.3529° (<http://www.sasscalweathernet.org>). The park is about 47000 ha in size, of which 46500 ha is on the plateau. The plateau can be seen in the far distance on the right from the tarred road between Okahandja and Otjiwarongo (Schneider, 1993).

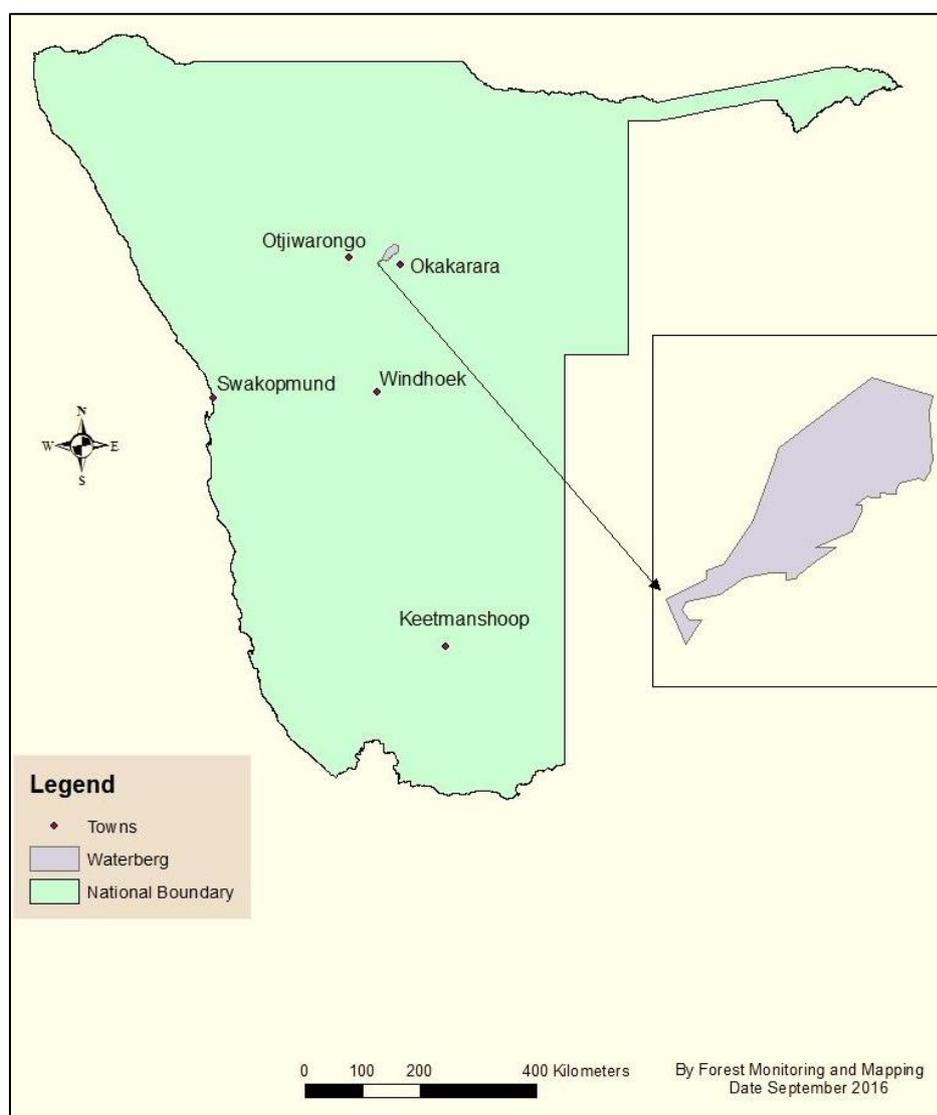


Figure 2.1: Location of Waterberg Plateau Park in central Namibia (Source: Forest monitoring and mapping, Ministry of Agriculture, Water and Forestry)

2.1.2 Physical features, geology and soils

The sandstone plateau is a prominent feature which is higher than 150 m above the surrounding thorn-bush savanna (Eco Impact Consultants, 2011; <http://www.nwr.com.na>). It is on average between 1550 m and 1850 m above sea level (Mukaru 2009). It extends about 50 km in length and 16 km in width (Eco Impact Consultants, 2011). The top of the plateau is made of lithified dunes, known as aeolianite, that belong to the Etjo formation, which forms part of the Karoo sequence. The sandstone plateau is about 200 million years old and is at least 100 m thick on the Waterberg (Schneider, 1993). Wind-blown Kalahari sand from the Kalahari basin in the east covers the brownish to light grey and medium grained sandstone, that is up to several meters deep (Mukaru, 2009; Eco Impact Consultants, 2011). The soil is very nutrient-poor as it was derived from red quartzite sand, which is heavily leached (Mukaru, 2009). Soil erosion and deposition is an important dynamic process in the park (Eco Impact Consultants, 2011).

2.1.3 Climate

The Waterberg Plateau Park is part of the “Hot steppe” climatic zone based on the Köppen system of classification (Erb, 1993). This means that the mean temperature is above 18 °C and the annual average number of days with rain is 40 – 50 (Erb, 1993). The topography of the park also has an influencing factor on the local climate of the plateau, which is between 100 m and 300 m higher than the surrounding plains (Erb, 1993).

The average daily minimum temperature for the coldest months is between 4 °C and 5 °C, where the temperatures during June can be as low as -5 °C (Erckie, 2007). The average daily maximum temperature in the hottest months ranges between 31 °C and 32 °C and from October to January it can reach 39.4 °C (Erckie, 2007). However, as recorded by the SASSCAL weather station on the plateau the average minimum temperatures for the cold period (May to September) for the years 2012, 2013, 2014 and 2015 were - 4.2 °C, - 3.6 °C, - 2.1 °C and -9.1 °C respectively. While the average maximum temperatures for years 2012, 2013, 2014 and 2015 were 31.5 °C, 32.7 °C, 30.4 °C and 36.5 °C respectively.

A mean annual rainfall measured below the plateau at Onjoka for the period 1981 to 2001 was 425.5 mm ± 129 mm (Eco Impact Consultants, 2011). More than 90% of the rainfall is between October and March, with February being the wettest month (Erb, 1993). The total rainfall amount for the years 2012, 2013, 2014 and 2015 as recorded by the SASSCAL weather station on the plateau was 664.1 mm, 395.7 mm, 838.2 mm and 81.6 mm respectively.

Dew and mist occur in summer and autumn respectively (Erckie, 2007). Frost occurs during winter on the plateau and this is associated with its topography, with a higher incidence of low temperatures occurring in the more low-lying areas (Erckie, 2007).

2.1.4 Flora

The Waterberg Plateau Park is part of the “Tree Savanna and Kalahari Woodland” vegetation types of Namibia, consisting mainly of a variety of deciduous trees and shrubs, and “hard” grass (Mukaru, 2009).

The important plant communities (adapted from Jankowitz (1983) as cited in the 2011 draft management plan by Eco Impacts Consultants (2011) are namely: the *Peltophorum africanum*, *Terminalia sericea* – *Blepharis integrifolia*, *Terminalia sericea* – *Melhania acuminata* and *Terminalia sericea* – *Thesium megalocarpum* communities. The *Peltophorum africanum* community occurs in the rocky areas, of the park, excluding the rocky areas on the Omuverume Plateau. The *Terminalia sericea* – *Blepharis integrifolia* community is a tree – shrub savanna on the dune crests, which is less affected by frost (Mukaru, 2009). It consists mainly of *Terminalia sericea*, but also *Burkea africana*, *Combretum collinum* and *Philenoptera nelsii* (Schneider, 1993). *Terminalia sericea* – *M. acuminata* community is also a tree – shrub savanna which is the largest and most widespread plant community in the park covering about 16 000 ha. The fourth plant community is the *Terminalia sericea* – *Lesium megalocarpum* which is also a tree – shrub savanna that occurs widespread on the deep sandy soils of the plateau, resulting in a complex mosaic distribution. It is associated with low-lying depressions (inter-dune valleys), which are prone to frost. Due to severe frost, trees in such areas rarely reach a height of more than four meters (Schneider, 1993).

Common trees in the park are *Acacia ataxacantha*, *Burkea africana*, *Combretum collinum*, *Combretum psidioides*, *Dichrostachys cinerea*, *Grewia flavescens*, *Grewia retinervis*, *Lonchocarpus nelsii*, *Ochna pulchra*, *Peltophorum africanum*, *Terminalia sericea* and *Ziziphus mucronata* (Erb, 1993).

Perennial grass species commonly occurring in the park are *Brachiaria nigropedata*, *Andropogon schirensis*, *Digitaria seriata*, *Eragrostis pallens*, *Eragrostis rigidior*, *Eragrostis jeffreysii* and *Panicum kalaharensis* (Erb, 1993).

2.1.5 Fauna

The Waterberg Plateau Park is an important conservation area and was proclaimed as park in 1972, with the main aim of protecting and breeding rare, endangered and economically important large herbivores (Schneider, 1993; Eco Impacts Consultants, 2011). Due to its

fairly inaccessible plateau the park is zoologically of special importance to Namibia, and hosts some of the endangered species such as the black rhino (*Diceros bicornis*), white rhino (*Ceratotherium simum*), roan antelope (*Hippotragus equinus*) and sable antelope (*Hippotragus niger*), are found (Mukaru, 2009). The above mentioned animals as well as the African buffalo (*Syncerus caffer*) are key species for the plateau, and are free of the foot and mouth disease virus (Eco Impacts Consultants, 2011). Most of the animals in the park were translocated into the park from other areas in the country to ensure their survival (Eco Impacts Consultant, 2011; Mukaru, 2009). Other large herbivores found in the park are giraffe (*Giraffa camelopardalis*), red hartebeest (*Alcelaphus buselaphus*), tsessebe (*Damaliscus lunatus*) eland (*Taurotragus oryx*), gemsbok (*Oryx gazella*), kudu (*Tragelaphus strepsiceros*), klipspringer (*Oreotragus oreotragus*), duiker (*Sylvicapra grimmia*), steenbok (*Rhaphicerus campestris*) and warthog (*Phacochoerus africanus*) (Erb, 1993). The animals were first translocated into the park at different intervals between 1975 and 1985 (Mukaru, 2009; Eco Impacts Consultants, 2011).

The park is free of large predators, apart from cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), brown hyena (*Hyaena brunnea*), and caracal (*Felis caracal*) (Mukaru, 2009; Eco Impacts Consultants 2011).

The park is also home to about 214 bird species (Eco Impacts Consultants, 2011), 30 species of small mammals, 81 reptile species and 13 amphibian species (Schneider, 1993; Eco Impacts Consultants, 2011).

2.2 Surveying outline

A space-for-time (SFT) substitution approach was used for this study as areas with different fire histories were surveyed. The SFT approach has widely been used and assumes that spatial and temporal variation are the same (Pickett, 1989). The initial and main aim of using SFT in ecology was to study plant succession, either because it was convenient or necessary (Pickett, 1989). It has traditionally been used for examining community structure and composition (Pickett, 1989).

To understand how fire history affects vegetation structure and species composition a total of four treatments (fire blocks) with different fire histories were surveyed and for frost effects one fire block burned 24 years ago but with some areas occurring in “interdunes” and others on higher elevation (dunes) was surveyed (Figure 3.1). In the fire history treatments, six 200 m long line transects were sampled. While in the frost occurrence (interdune & dune) treatment, twelve 100 m (to avoid overlapping due to small area) long line transects were sampled. All transects and the first sampling points on each transect were randomly

selected. GPS coordinates were taken at every sample point on all transects (Appendix 1). Along the 200 m line transects 5 points were surveyed at 40 m intervals, while on the 100 m transects 3 points were surveyed. At every survey point the following sampling techniques were used: the point centred quarter method, the Bitterlich gauge and the visual obstruction reading (Robel pole) method.

CHAPTER 3

EFFECTS OF FIRE HISTORY ON VEGETATION STRUCTURE AND SPECIES COMPOSITION IN A SEMI-ARID SAVANNA WOODLAND

3.1 Introduction

The association between fire and savannas is as old as the savannas themselves, and fire is inevitable (Scholes & Walker, 1993), regardless of management intentions. Savanna climatic characteristics (dry and wet periods) make them highly prone to fire due to lightning storms and extended dry periods (Trollope, 2003; Scholes & Walker, 1993). The widespread occurrence of fire in Africa, especially in the savanna and grassland biomes brands it as the fire continent (Komarek, 1971 in Trollope, 2003). This is largely due to widespread anthropogenic fires that often burn savanna vegetation annually (Sheuyange et al., 2005), which has increased with the expansion of the human population (Mapaure & Moe, 2009). This has led to grasslands and savannas extending at the expense of evergreen forests (Trollope, 2003). Also, human beings over the years have altered the natural fire regime and created various fire histories. Thus, fire (natural or human-induced) is an influential ecological phenomenon that cannot be disregarded when considering the management of rangelands for both domestic livestock and wildlife purposes (Trollope, 2003).

Fire is one of many variables in combination with other environmental drivers, such as rainfall, herbivory and human activities affecting African savanna vegetation (Burke, 2006). Fire may slow down regeneration and recruitment of woody plants; however it promotes establishment and maintenance of herbaceous component by preventing growth of taller, fire-resistant stages of woody plants (Mapaure & Moe, 2009). In an arid Namibian savanna, Joubert et al. (2012) predicted that fire, although not frequent and generally cooler (low fuel loads) than in more wet savannas, is necessary in keeping savannas in an open grassy state when they occur at the time of seedling establishment. In arid savannas, the most evident results of fire are the removal of litter layer on the soil surface, moribund material and the alteration of microclimates and nutrient levels on the surface soil, as pointed out by Frost (1985) in Nepolo & Mapaure (2012). Surface fires are the most common type of fire in southern African savannas and are fuelled largely by grass (Burke, 2006). They damage vegetation within flame height, usually less than 2 metres (Burke, 2006). Most savanna woodland vegetation is well adapted to fire through its ability to vigorously resprout and regrow (Smit, Asner, Govender, Bowdoin, Knapp, & Jacobson, 2010; Burke, 2006). The main impacts of fire on woody vegetation structure are the suppression of tree recruitment and the prevention of most trees from reaching a height (> 2 m) which would allow them to escape

the flame zone (Burke, 2006) or more critically a thicker bark or bigger stem diameter. Therefore, vegetation structure should be a good indicator of past fire regimes (Burke, 2006) in an area. Fire is considered to be one of the key management tools that have and can be used to manipulate woody vegetation structure (Smit et al., 2010).

3.2 Literature review

In all fire-prone ecosystems, fire is dependent on the availability of fuel load (Accantino et al., 2010). Fuel load influences the occurrence and spread of fires, and it is in turn influenced by rainfall and herbivory, in that adequate rainfall and/or low herbivory lead to grass biomass accumulation (Accantino et al., 2010).

To understand the effects of fire in an area, it is important to know the fire regime of that area. Frequency, intensity, season of burning and type of fire that prevails in a given area are the four main components of a fire regime (Scholes & Walker, 1993; van Wilgen, Andreae, Goldammer, & Lindesay, 1997; Brockett, Biggs & van Wilgen, 2001; Trollope, 2003; Driscoll, et al., 2010). Human beings have greatly altered fire regimes ever since they have been using fire (Eco Impacts Consultants, 2011). In Namibia, in the north eastern part for example, fire frequencies have been increased by humans to such an extent that some areas are burned almost annually for agricultural purposes (Eco Impacts Consultant, 2011). In other areas of the country however, especially in commercial farming areas, fire frequencies have been greatly reduced either intentionally or as a result of reduced fuel load or both, this is said to have increased woody species density and cover (Eco Impacts Consultants, 2011). The effects of fire depend mainly on the intensity and frequency of fires which is influenced by the physical characteristics of the fuel load (Sheuyange et al., 2005), as well as relative humidity, fuel moisture, wind speed, and slope (Trollope, Trollope & Hartnett, 2002).

After an area is burned the post-fire vegetation composition is dependent on the pre-fire composition, but it can vary significantly away from it (Morrison, Cary, Pengelly, Ross, Mullins, Thomas & Anderson, 1995). Generally, species richness and diversity tend to increase immediately after a fire and then gradually decrease (Morrison et al., 1995). Initial regrowth is usually by fire-tolerant species whose adult plants survive the fire and resprout, while the fire-sensitive species whose adult plants do not normally survive tend to contribute more to the above-ground community after some years in the absence of fire (Morrison et al., 1995).

Fire frequency is defined as a function of the number of fires experienced in a particular community over a certain time period (Gill, 1975 in Morrison et al., 1995). It refers to how often an area burns and this is one of the important characteristic of a fire regime (Gandiwa,

2011). The effects of fire frequency on vegetation can be separated into two variables: the shortest time interval between fires and the time since the last fire (Nieuwenhuis, 1987 in Morrison, et al., 1995). How often an area burns affects how that ecosystem functions in terms of nutrient cycling, grass productivity, tree recruitment and mortality (Gandiwa, 2011). For example, an average fire frequency of every 3-10 years is reported for Etosha National Park (van Wilgen et al., 1997) which has a mean annual rainfall ranging from 250-500 mm (Zimmerman, Higgins, Grimm, Hoffmann & Linstadter, 2010). Burning frequency has differing effects on grass composition, as frequent burning may favour some species and infrequent burning may favour other species (Trollope, 2003). Frequent burning temporarily improves and maintains the nutritional quality of rangelands making it highly attractive to grazing animals, especially in high rainfall areas (Trollope, 2003). Large herbivores prefer feeding on this post-fire grass regrowth compared to dead plant material that has not been burned (Mbatha & Ward, 2010; Zimmerman et al., 2010), decreasing the frequency of fires in these areas due to reduced fuel load. Several studies (Mapiye, Mwale, Chikumba, & Chimonyo, 2008; Bothma & du Toit, 2010; Mbatha & Ward, 2010; Eco Impacts Consultant, 2011) found that fire increases grass quality in the short term as it removes moribund material resulting in young growth of grass tissue. New grass shoots in recently burned areas had higher crude protein content than dry grass in an unburned area in the Waterberg Plateau Park (Erb, 1993).

Fire also changes grass species composition often towards more palatable species (Scholes & Walker, 1993). Grasses differ in their grazing value or quantity and quality of material they produce for grazing (van Oudtshoorn, 2004). Grazing value is influenced by several factors, but palatability and production of grasses are the key factors (van Oudtshoorn, 2004). Production is the ability of grass to produce a certain amount of leaf material, while palatability refers to the nutritional value and digestibility of grasses (van Oudtshoorn, 2004). The grasses with high grazing value are usually Decreaser species, which are those perennial grasses that decline in a veld with overgrazing or under-utilisation (van Oudtshoorn, 2004). While Increaser species increase in overgrazed or underutilised veld and fall in the average and low grazing value category (van Oudtshoorn, 2004). If fire occurs too frequently it decreases quality and quantity of grasses because of its negative impact on stored reserves (Mbatha & Ward, 2010). Perennial grasses are an essential component of many vegetation formations as they provide important ecosystem services such as forage for herbivores and prevent soil erosion (Zimmermann et al., 2010) and thus their conservation is crucial.

Few studies (Geldenhuys, 1977 & Rutherford, 1981 in Burke, 2006; Gandiwa, 2011) have been done that focus on how fire affects vegetation composition in savannas, especially in

southern Africa. Studies done in Australian savannas found that frequent fires lead to the local extinction of fire-sensitive species as these species do not reach their first reproduction (the primary juvenile period). Similarly, new individuals of fire-tolerant species will not be recruited to the population if fires are too frequent for plants to reach post-fire reproduction (the secondary period) as well as the time taken by juvenile plants to reach fire-tolerant sizes (Morrison et al., 1995). Therefore, the susceptibility of the different species to disturbances such as fire influences the community composition over time (Holdo, 2007). Observations of high disturbances (frequent fires, killing-frost events and high elephant numbers) in the Kalahari woodlands in the Hwange area show a scrub vegetation dominated by more fire resistant species such as *Ochna pulchra* (Holdo, 2007). In mature *Baikiaea* woodlands however, the composition may not change but it may eventually shift to a stable scrub phase as woody plants are confined in the fire trap (Holdo, 2007).

There are conflicting findings on the effect of frequency of burning on density of woody vegetation. Van Wyk ((1971, in Gandiwa (2011)) suggested that there is no significant effect of frequency of burning on woody plants density. Trollope (2003) also found no significant changes in bush density in response to different burning frequencies in Kruger National Park (KNP). Contrary to this, annual burning in Botswana and Zimbabwe resulted in significant reductions in the density of bush than less frequent burning (Boulton & Rodel, 1981; Sweet, 1982 in Trollope, 2003). Smit et al. (2010) showed that fire frequency acts largely on the shorter height classes, thus a lower density of bush as compared to less frequent fires. This is because less frequent fires allow more woody vegetation to escape the flame zone due to a longer recovery period (Smit et al., 2010). However, Trollope (2003) suggested that the effect of frequency of burning on woody vegetation depends rather on the type and intensity of fire.

While fire may alter structure and maintain savanna ecosystems, it can cause considerable losses of nutrients that are required by plants from the soil to the atmosphere, with losses of nitrogen through volatilization being more than those of other nutrients (Cech et al., 2008; Holdo, 2013). Therefore, frequent fires may promote a shortage of nitrogen, and many savannas are thought to be primarily nitrogen limited (Cech et al., 2008).

Another component of the fire regime that is thought to be more important than fire frequency despite the difficulty to measure it is fire intensity (Trollope, 2003). Fire intensity is defined as the release of heat energy per unit time per unit length of fire front (Scholes & Walker, 1993; van Wilgen et al., 1997; Trollope et al., 2002; Trollope, 2003). Amount of fuel load, fuel moisture, relative humidity and wind speed are some of the variables that influence how intense a fire is (Trollope et al., 2002).

Fire intensity apparently has no significant effect on the recovery of grass after a burn (Trollope & Tainton, 1986 in Trollope, 2003). However, fire intensity strongly affects tree mortality in savannas as well as the recruitment of trees into larger size classes (Govender et al., 2006) and managers have used this knowledge to reduce tree dominance and encroachment by applying conditions that lead to more intense fires. Fire generally kills seedlings of woody plants as they are easily flammable (Accantino et al., 2010; Joubert et al., 2012), which could be due to the majority being small and lacking strong physical protection, such as a thick bark (Chidumayo, 2013). Therefore, fire acts as a bottleneck in tree demography preventing canopy closure (Accantino et al., 2010) and thus maintaining an open savanna. To maintain an open savanna, burning should be in the drier months when conditions are favourable for high intensity fires and when the dormancy of woody plants is broken (Wiegand et al., 2006; Chidumayo, 2013). During this time woody plants are more prone to being killed or top-killed as their growth buds are exposed (Wiegand et al., 2006; Chidumayo, 2013) and their food reserves are depleted due to new spring growth (Gandiwa, 2011). Woody plants that are top-killed during the fire usually resprout from the base to replace above-ground biomass (Govender et al., 2006). Therefore, in the drier months, fire in savanna ecosystems affects the woody component through killing seedlings and by limiting the recruitment of tree saplings to adults, and favouring the grass component (Wiegand et al., 2006; Joubert et al., 2012; Nepolo & Mapaure, 2012; Chidumayo, 2013).

Season of fire refers to the time of the year that burning occurs, in relation to the growth state of the vegetation (van Wilgen et al., 1997). Fire in Southern African savannas occurs mainly in the dry season when the perennial grasses are dormant (Accatino et al., 2010). Trollope (2003) in the KNP found that lightning fires occur mostly during October to January when thunderstorms are most frequent, whereas anthropogenic fires mainly occur during June to September just before the rainy season. During this dry period fire burns away grass leaves as fuel without generally killing the dormant grass buds at or below the soil surface and also burns tree leaf litter (Accatino et al., 2010). Trollope (2003) thus advises it is important to burn when the grass is dormant in late winter or just after the early rains. In contrast, if burning takes place late in the growing season when grass is actively growing, it causes a high mortality and a reduction in abundance of species (Trollope, 2003). At this time grass tillers are actively growing and shoot apices are therefore probably elevated and in a vulnerable position to be damaged by the fire (Trollope, 2003). Thus, the effect of burning on grass depends on the physiological state of the grass at the time of the fire.

Savanna woody vegetation is well-adapted to fire (du Toit et al., 2003; Trollope 2003; Goldammer & de Ronde, 2004; Bothma & du Toit, 2005; Mills & Fey, 2005; Smit et al., 2010). Most savanna woody plants are not completely killed by fire, but only stem mortality occurs

(du Toit et al., 2003; Trollope, 2003; Bothma & du Toit, 2005; Holdo, 2005). Instead of massive above-ground growth after disturbances such as fire, woody plants allocate resources below ground (Bond & Midgley, 2001; Wakeling, Cramer & Bond, 2012). This strategy enables woody plants to resprout from the base, a key life-history trait that promotes the persistence of trees in savannas (Higgins et al., 2000; du Toit et al., 2003; Trollope, 2003). Trollope (2003) from his findings of a study done in the arid savannas of the Eastern Cape and KNP, concluded that in general, the main effect of fire on woody plants in the savannas is to cause a top-kill of stems and branches forcing the plants to coppice from the base of stems from surviving meristems and stored reserves. The persistence of resprouting woody plants is referred to as gullivers by Bond & van Wilgen (1996) in Higgins et al. (2000). Fire this way maintains woody plants at browsable heights for shorter herbivores (Trollope, 2003; Bothma & du Toit, 2005; Joubert et al., 2012).

Small trees are more vulnerable as they may be entirely within the flame zone, whereas mature trees are less affected due to their thick bark and their buds (dormant in the fire season) that are held above the flame zone (Accatino et al., 2010). As mentioned above, trees and shrubs are probably more adversely affected by fire at the end of the dry season when the plant reserves are depleted due to the new spring growth and when there is a lot of fuel load supporting intense fires because of high temperatures, low humidity and low moisture content (Trollope, 2003), which emphasizes that frequency, season and intensity are all linked. Several studies (Trapnell, 1959 and Kenan, 1971 in Smit et al., 2010) found that burning in the dry season (October) had more drastic effects on regeneration and regrowth of woody vegetation than burning early in the dry season (June/July). However, a study in KNP showed that mortality of bush was very low after fires were applied to bush ranging from dormant to actively growing plants, thus suggesting that bush is not sensitive to season of burn (Trollope, 2003). With regard to woody vegetation cover, it is reduced more by long-term exposure to dry-season fires than by wet-season fires, as the former are of higher intensity (Smit et al., 2010). It is therefore difficult to determine the effect of season of burning on woody vegetation as it is determined more by fire intensity (Trollope, 2003).

In grassland and savanna areas the most common types of fires are surface fires that burn either as head or back fires (Burke, 2006, Trollope, 2003; Trollope et al., 2002; Scholes & Walker, 1993). Trollope (2003) and Trollope et al. (2002), stated that the significance of the effect of type of fire on plants is that it determines the vertical level at which heat energy is released in relation to where the bud tissues are from which meristematic sites are for the plants to recover after burning. Crown and surface head fires burning with the wind caused the highest top-kill of stems and branches in the KNP and Eastern Cape, as compared to back fires burning against the wind (Trollope et al., 2002). However, for grasses, in the study

that was conducted in the arid savannas of the Eastern Cape, more heat was released at ground level during back fires than during head fires, therefore the shoot apices of the grass plants were more adversely affected during the back fires (Trollope (2003).

Fire regimes are a major determinant of savanna vegetation composition, structure and dynamics. Some advantages of fire are that it can remove moribund material, improve forage quality, reduce woody cover through top-kill or prevent encroachment of undesirable plant species thus maintaining open savannas. However, the effects of fire depend on previous rainfall, soil texture, amount of fuel load, density of grazers and browsers and life stages of the present vegetation among other factors (Wiegand et al., 2006).

For the purpose of this study fire history only took into account fire frequency and time since last burn, as there is no information on other fire regime components for the study area. However, the effects of fire frequency, time since last burn and grazing pressure are discussed, relating them to the potential fire intensity.

3.3 Key research objectives, questions and hypotheses

The specific objectives of the study were to compare the effects of different fire histories at the Waterberg Plateau Park on the following:

- (a) vegetation density
- (b) grass biomass
- (c) grazing value of perennial grasses
- (d) woody cover and
- (e) species composition

The study sought to answer the following questions: How does fire history affect the following:

- (a) vegetation density
- (b) grass biomass
- (c) grazing value of perennial grasses
- (d) woody cover and
- (e) species composition

The research hypotheses of the study were:

- (a) In the absence of fire individual perennial grass tufts grow bigger and competition between these tufts intensifies, as well as competition with the woody component, which is usually a stronger competitor. Thus, perennial grass density declines with

increasing time since last burn, while woody density increases with time since last burn.

- (b) Grass biomass is significantly lower in the recently burned areas. Fire burns away dry and moribund grass, the resulting new grass shoots are more palatable and readily grazed. In addition, the new individual grass shoots that regrow after a fire have small tufts as compared to treatments which are not burned recently in which the grass tufts have had enough time to grow bigger.
- (c) Relative density of palatable perennial grass species is positively affected by fire, whereas the relative density of less palatable species is negatively affected by fire.
- (d) Woody canopy cover is positively affected by fire interval and increases with time since last burn. This is because fires open up canopies by causing top-kill of woody vegetation and thus creating open savannas. Frequent fires will cause more open areas than less frequent fires.
- (e) Perennial grass and woody species composition in savannas is influenced among other factors by fire and soil nutrients. Fire history shapes savanna vegetation structure such that recently burned areas will have higher relative density of grasses but a lower relative cover of woody plants.

3.4 Data collection

3.4.1 Surveyed treatments

The study was carried out in four fire blocks (approximately 2000 ha each) (Figure 3.1; Plate 3.1-3.4) with mean fire return intervals ranging from 6.2 years to 18.5 years and time since last burn ranging from 1 year ago to 24 years ago at the time of data collection to provide an understanding on how fire history affects vegetation structure and species composition (Table 3.1). The treatments will be referred to by the number of years since they were last burned, as follows: 1, 2, 14, and 24.

Table 3.1: The surveyed treatments with their mean fire return interval and time since they were last burned (Joubert, 2013: unpublished data)

Treatment	Mean fire return interval (years)	Time since last burn (years)
1 (1)	6.2	1
2 (2)	9.3	2
3 (14)	9.3	14
4 (24)	18.5	24

Note: The number of years for time since last burn was at the time of data collection in 2014.

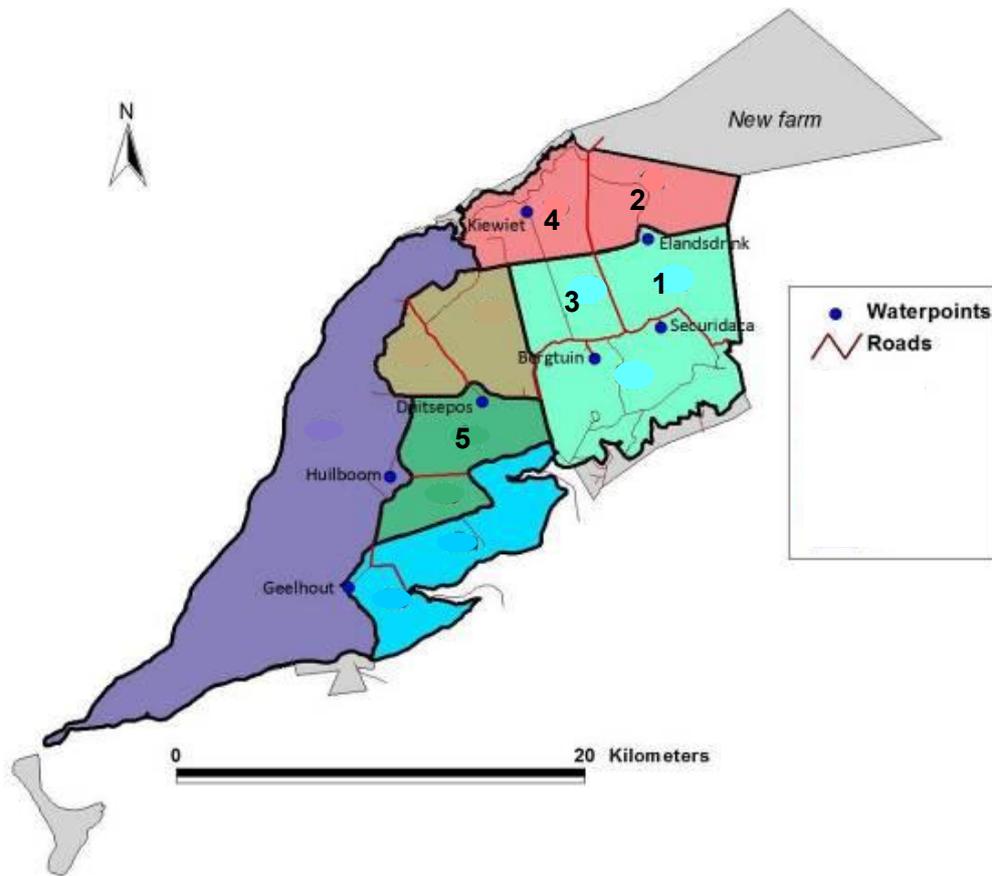


Figure 3.1: Location of the surveyed treatments in the Waterberg Plateau Park (Source: Eco Impacts Consultants, 2011)



Plate 3.1: Treatment that was burned 1 year ago (Image: D.F. Joubert)



Plate 3.2: Treatment that was burned 2 years ago (Image: D.F. Joubert)



Plate 3.3: Treatment that was burned 14 years ago (Image: N. Uunona)



Plate 3.4: Treatment that was burned 24 years ago (Image: D.F. Joubert)

3.4.2 Sampling methods

In each of the treatments six 200 m line transects were randomly placed. Along each transect five points at 40 m intervals were surveyed as follows:

(a) Estimating vegetation structure using the PCQ method

The PCQ method is a plot-less method developed and described by Cottam and Curtis (1956) for conducting vegetation surveys. In a study area where the vegetation is very dense, the PCQ method allows for rapid estimates by using a series of measurements along a transect(s) (Mitchell, 2007).

The PCQ method used to survey the vegetation is an adapted version by Trollope, Trollope, Goode, de Bruyn & van den Broeck (2013) from Cottam and Curtis (1956), which overcomes the problems linked with area based methods such as belt transects and quadrats that result in over sampling small, short woody plants and under sampling taller trees and shrubs. In each quarter within a 20 m radius (Trollope et al., 2013), the distances to the nearest live perennial grass and to woody species of <1 m, 1-2 m, 2-3 m, 3-4 m and >4 m were measured using a measuring tape and recorded. The basal diameter of the perennial grasses and the height of the woody plants were also measured (Plate 3.5). The different species being measured were also identified, and if they were not known in the field they were collected and pressed for later identification with the help of experts and/or identification manuals.

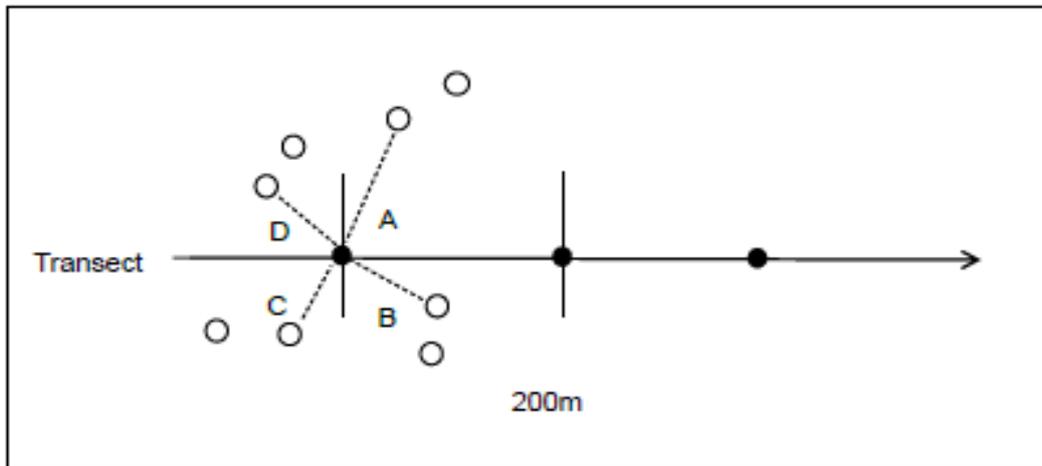


Figure 3.2: Illustration of how the PCQ method works (Adapted from Mitchell, 2007)



Plate 3.5: Image showing how height of woody plants was estimated using a 2 m pole (Image: S. Lutibezi)

(b) Estimating grass biomass using the VOR (Robel pole) method and grass clipping

The VOR (Robel pole) technique is used to estimate the biomass of vegetation present at the time of measurement (Smith, 2008; Uresk, Mergen, & Benzon, 2009). It is a reliable, consistent, cost effective method that covers a large area in a short amount of time (Smith, 2008). In addition, once the relationship between VOR and standing biomass has been established, Robel pole use requires little effort to monitor rangelands (Uresk et al., 2009).

Joubert, Powell & Schacht (2014) tested this technique in Namibia, including in the Waterberg Plateau Park. This method requires two people. In every quarter B of the PCQ, a measuring tape was used to measure 5 m away from the PCQ. This was done to avoid the disturbed area around the PCQ made while taking other measurements. At this point, one person stood holding a 2 m pole on the soil surface subdivided into 2.5 cm rings with alternating red and white bands, as shown in Plate 3.6. VORs were made from a distance of 4 m with the reader's eye at a height of 1 m (Uresk et al., 2009). The lowest visible band completely obscured by perennial grasses was identified and the number of bands obstructed by grasses was counted and recorded. Four VORs were recorded at each PCQ point in each cardinal direction. In the cases where woody plants obstructed the pole, the person moved left or right to avoid this. The dominant perennial grass species that contributed to the obstruction of the pole were also identified and recorded.

The VOR were calibrated with actual biomass readings from 60 points occurring in the treatments burned 2 years and 24 years ago. In a 1 m² quadrant at the VOR point, all the grasses in it were clipped using secateurs about 5 cm above the ground. The grass clipped was placed in brown paper bags and later dried in a drying oven at 60 °C for 48 hours. Thereafter, the dry grass samples were weight using an electronic balance.



Plate 3.6: Image showing how the Robel pole method works to determine grass cover (Image: D.F. Joubert)

(c) Estimating woody cover using the Bitterlich gauge

The Bitterlich gauge (Figure 3.3) is the recommended method for measuring canopy cover of woody plants in a wide area (Friedel & Chewings, 1988 in Zimmermann & Mwazi, 2002). The tip of the longer rod is held below the eye, with the other tips held horizontally in the direction of a woody canopy. If the woody canopy extends beyond the two tips (Plate 3.7), the canopy is counted and recorded as 1 (then converted to percentage by multiplying with the percentage factor of 5 in this case) and its species identified, if the two tips extend beyond the canopy (Plate 3.8) then it is ignored. This procedure was repeated until a 360° turn clockwise was made at every PCQ point along each transect. Only the canopies of living individuals that extend beyond the two tips of the gauge were recorded. For overlapping canopies of different species, only the dominant species was recorded for that canopy.

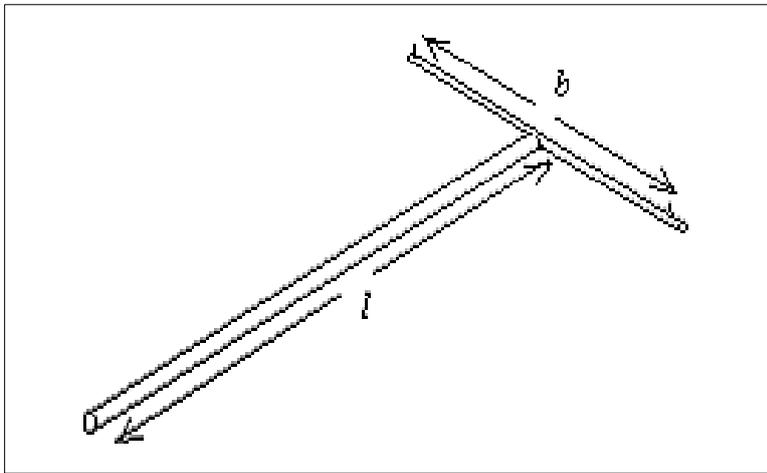


Figure 3.3: Illustration of the Bitterlich gauge, with dimensions $l = 75$ cm and $b = 33.5$ cm (Source: Friedel & Chewings, 1988 in Zimmermann & Mwazi, 2002)



Plate 3.7: Bitterlich gauge pointed at a woody canopy to estimate woody cover. In this photo, the tree canopy was recorded (Image: D.F Joubert).



Plate 3.8: Bitterlich gauge pointed at a woody canopy to estimate woody cover. In this photo, the tree canopy was not recorded. (Image: J.A.N Kandjai)

3.4.3 Data analysis

The statistical software package STATISTICA 12 (StatSoft, 2002) was used to run all statistical tests. The Kolmogorov-Smirnov test was used to see if data were normally distributed. The main effects analysis of variance (ANOVA) revealed that time since last burn was the driving variable contributing to significant differences as compared to mean fire

return interval, and hence time since last burn was considered the driving variable for all further tests. For normally distributed data the one way ANOVA was used. If the one way ANOVA yielded a significant difference, Fisher's less significant difference (LSD) post-hoc test was used for multiple comparisons among treatments to reveal which treatments were different. If the data were not normally distributed, the equivalent non-parametric Kruskal-Wallis test was used to test for significant differences, after which the Mann-Whitney test was performed to reveal which treatments were different. For all statistical tests, the mean of all variables per transect was used as a sample and not each point as the points along transects were not randomly placed but transects were.

(a) Vegetation density

The distances from the PCQ points to the perennial grasses and woody plants were used to calculate their density. The density of the perennial grasses and woody plants was calculated using the following formula:

$$\text{Density} = 1 / (\text{average distance in meters})^2 \text{ (Mitchell, 2007)}$$

The density was calculated as individuals per hectare. The mean density per transect in all the treatments was used as a sample. For woody plants density was calculated per height class as well as mean total density.

(b) Grass biomass

The VOR readings and the dry weight were plotted as a scatter plot and a regression line was obtained from this (Appendix 4). The obtained regression equation was used to convert the VOR results into grass biomass:

$$y = 65.026x + 20.123, \text{ with } R^2 = 0.558$$

Where y = biomass in grams, x = VORs as number of ring bands obstructed by grass

The mean grass biomass per transect in all the treatments was calculated as kilograms per hectare.

(c) Grazing value of perennial grass species

The different grass species were classified into the following grazing value categories: High grazing value, average grazing value and low grazing value using a published index by (Muller, 2007) (Appendix 5). The mean relative density for each grazing value category in all treatments was calculated as follows:

$$\text{Relative density} = (n_i / \sum n) * 100$$

Where n_i = number of individuals of each species and $\sum n$ = total number of all individuals

(d) Woody cover

The number of hits obtained in the field using a Bitterlich gauge with dimensions $l = 75$ cm and $b = 33.5$ cm were converted to percentages by multiplying them by 5 (correction factor). The mean woody cover was calculated per height class in each transect as well as mean total woody cover. To test for significant differences between the four treatments with different years of time since last burn, Kruskal-Wallis test was used. The Mann-Whitney test was performed afterwards to reveal which treatments were different.

(e) Species composition

A hierarchical cluster analysis (HCA), using Euclidean distance measure with Ward's linkage method was performed on a plots-by-species matrix, using weighted data in PC-ORD 6 (McCune & Mefford, 2011). This was done separately for perennial grass species (relative density) and woody species (relative woody cover). The aim of a cluster analysis is to assign sample units to discrete groups with different levels of similarity (McCune & Grace, 2002). The information is then presented as a dendrogram diagram showing the resulting hierarchical grouping structure (McCune & Grace, 2002).

The different treatments were also compared by performing a non-metric multidimensional scaling (NMS) ordination in PC-ORD 6 (McCune & Mefford, 2011) on the same data set. Ordination as defined by McCune & Grace (2002) is a method of graphically summarising complex relationships, extracting one or few dominant patterns from infinite possible patterns. In community ecology ordination is used mainly to describe the strongest patterns in species composition. This is done based on the fact that species abundance differs along environmental or historical gradients (McCune & Grace, 2002). Therefore, ordination orders sampled units along gradients.

The NMS was run on weighted data for both perennial grass species composition (relative density) and woody species composition (relative woody cover). The environmental variables used in the ordination were: time since last fire, mean fire return interval and the following soil properties provided by Nghalipo, (2016): clay %, organic carbon, phosphorus, potassium, calcium, magnesium, sodium, and nitrogen. Sorenson distance measure was used with a random seed supplied by the user. From the scores of the ordination, joint plots were used to show the findings. Joint plots show the relationship between a set of environmental variables and ordination scores as a diagram with radiating lines (McCune & Grace, 2002).

3.5 Results

(a) Vegetation density

i. Perennial grass density

Mean perennial grass density decreased significantly with time since last burn ($F=5.568$, $df=3$, $P<0.05$, $n=6$) (Figure 3.4). Treatment 1 had about three times higher perennial grass density than treatments 14 and 24.

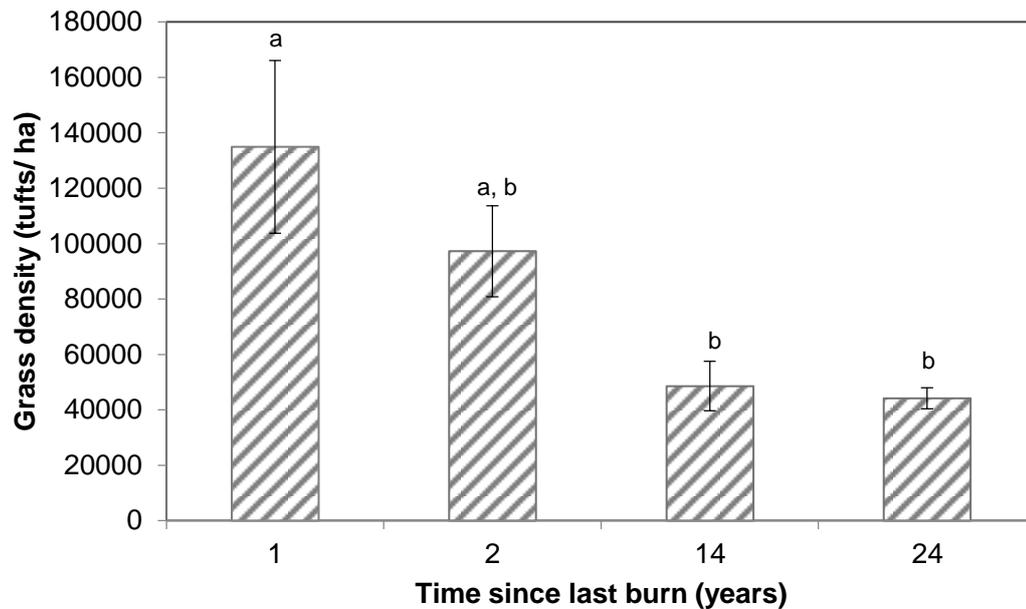


Figure 3.4: Perennial grass density (grass tufts/ ha) in relation to time since last burn (years). Letters denote significant differences between treatments, while the bars show standard errors.

ii. Woody density

Mean total woody density was not statistically different ($F=1.004$, $df=3$, $P>0.05$, $n=6$) among treatments with different years of time since last burn (Figure 3.5). There were however significant differences ($F=5.416$, $df=15$, $P<0.05$, $n=6$) found among treatments in all height classes. Woody density in the height class <1 m was higher in treatment 2 than treatment 24 (Figure 3.6a). In the 1-2 m height class woody density in treatment 1 was significantly lower than for all other treatments (Figure 3.6b). In the height classes 2-3 m and 3-4 m treatment 24 had higher woody density than for all other treatments (Figure 3.6b & 3.6c). For >4 m height class, treatment 1 and treatment 14 had higher woody density than treatments 2 and 14 had more woody density than treatment 24 (Figure 3.6c).

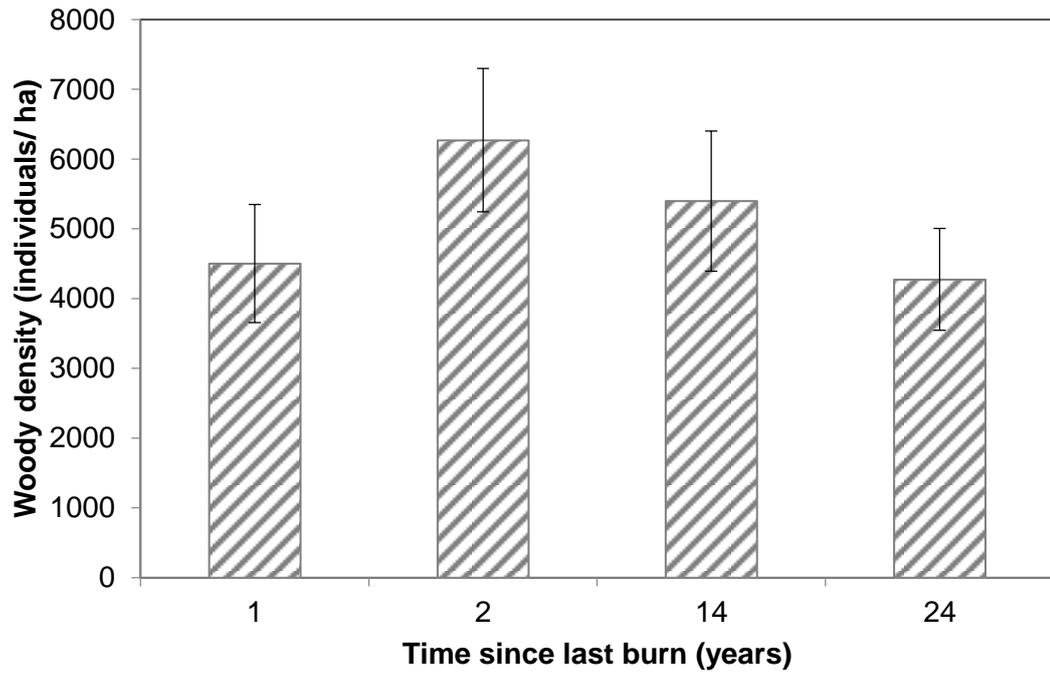


Figure 3.5: Total woody density (individuals/ ha) in relation to time since last burn (years). The bars show standard errors.

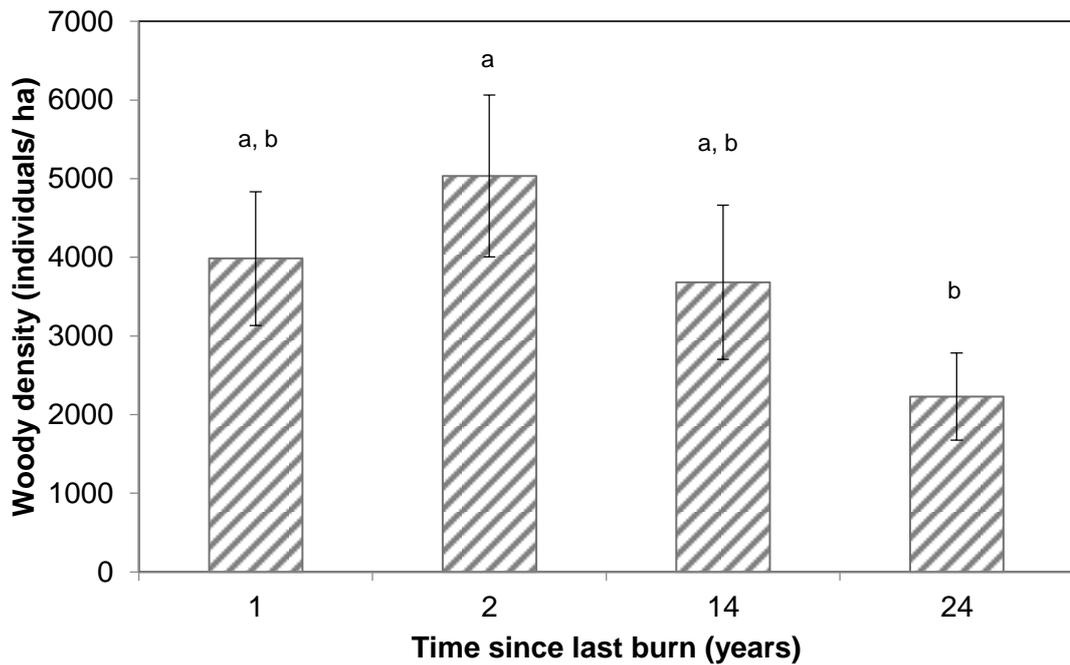


Figure 3.6a: Woody density (individuals/ ha) in height class < 1 m in relation to time since last burn (years). Letters denote significant differences between treatments, while the bars show standard errors.

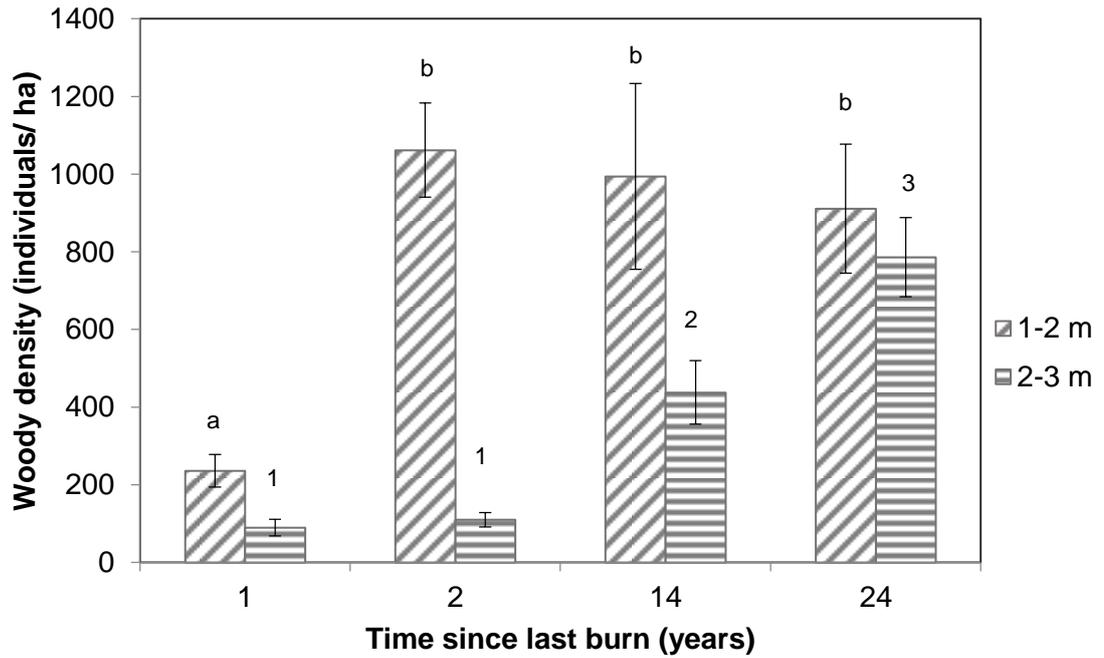


Figure 3.6b: Woody density (individuals/ ha) in height classes 1 m – 2 m and 2 m -3 m in relation to time since last burn (years). Letters and numbers denote significant differences between treatments, while the bars show standard errors.

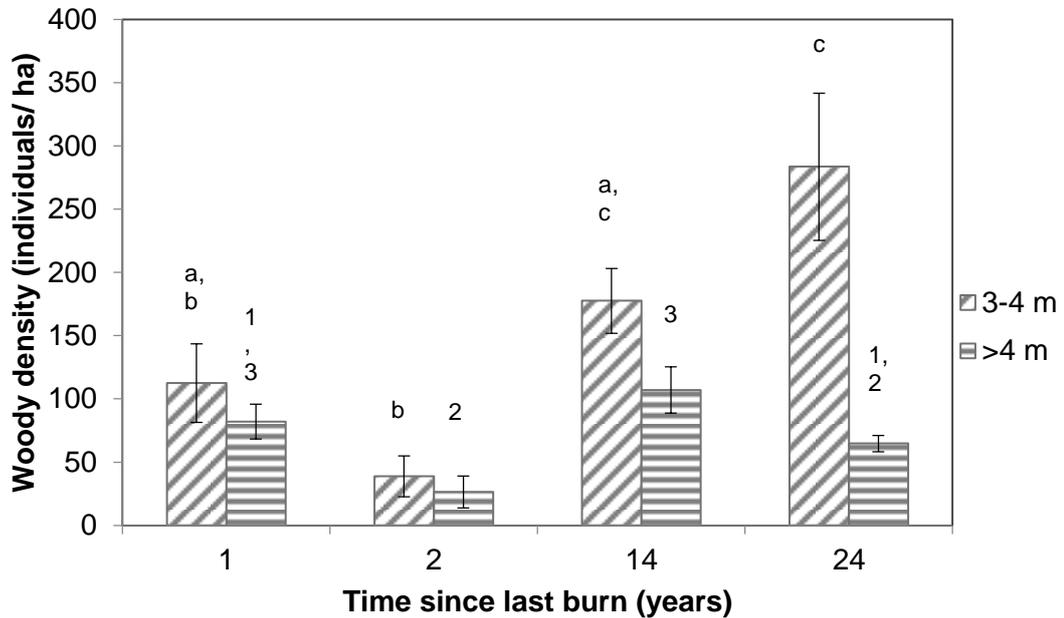


Figure 3.6c: Woody density (individuals/ ha) in height classes 3 m – 4 m and >4 m in relation to time since last burn (years). Letters and numbers denote significant differences between treatments, while the bars show standard errors.

(b) Grass biomass

Mean grass biomass was found to be significantly different ($F= 4.611$, $df= 3$, $P < 0.05$, $n=6$) between treatments with different years of time since last burn. Treatment 2 had about three times higher mean grass biomass than treatment 1 (Figure 3.7).

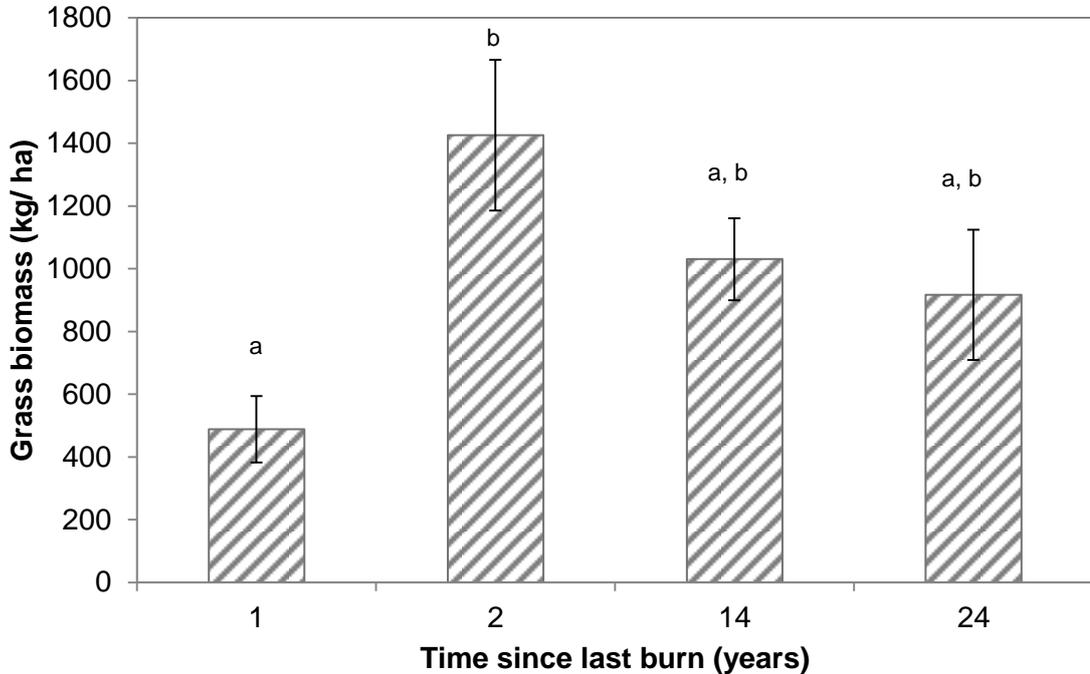


Figure 3.7: Grass biomass (kg/ ha) in relation to time since last burn (years). Letters denote significant differences between treatments, while the bars show standard errors.

(c) Grazing value of perennial grasses

Mean relative density in each grazing value category was found to be significantly different ($P < 0.05$) among treatments with different years of time since last burn (Figure 3.8). Treatments 1 and 2 had a higher relative density of high grazing value grass species than 14 ($F= 3.383$, $df= 3$, $P < 0.05$, $n=6$) and a lower relative density of the average grazing value grass species. In the average grazing value category treatment 14 had higher relative density than all the other treatments ($P < 0.05$). There were no significant differences among treatments in the low grazing value category ($F= 0.432$, $df= 3$, $P > 0.05$, $n=6$).

Only 3 grass species of high grazing value were encountered with *D. seriata* having the highest relative density overall and mostly in the recently burned areas (Table 3.2).

Table 3.2: Relative density (%) of perennial grass species with grazing value in relation to time since last burn (years)

Perennial grass species	Grazing value	Treatment			
		1	2	14	24
<i>B. nigropedata</i>	High	0	9.2	0.8	0.8
<i>D. seriata</i>	High	57.5	44.2	26.7	44.2
<i>P. maximum</i>	High	1.7	0	0	0
<i>A. meridionalis</i>	Average	2.5	0.8	0	0.8
<i>E. lehmanniana</i>	Average	0.8	0	1.7	0
<i>M. repens</i>	Average	0.8	0	2.5	1.7
<i>P. kalaharensis</i>	Average	2.5	7.5	11.7	5
<i>S. uniplumis</i>	Average	5	5	14.2	2.5
<i>T. schinzii</i>	Average	0.8	0	3.3	5.8
<i>A. stipitata</i>	Low	18.3	23.3	20	22.5
<i>E. jeffreysii</i>	Low	3.3	2.5	12.5	0.8
<i>E. pallens</i>	Low	5.8	4.2	2.5	12.5
<i>S. hirtigluma</i>	Low	0	3.3	4.2	3.3

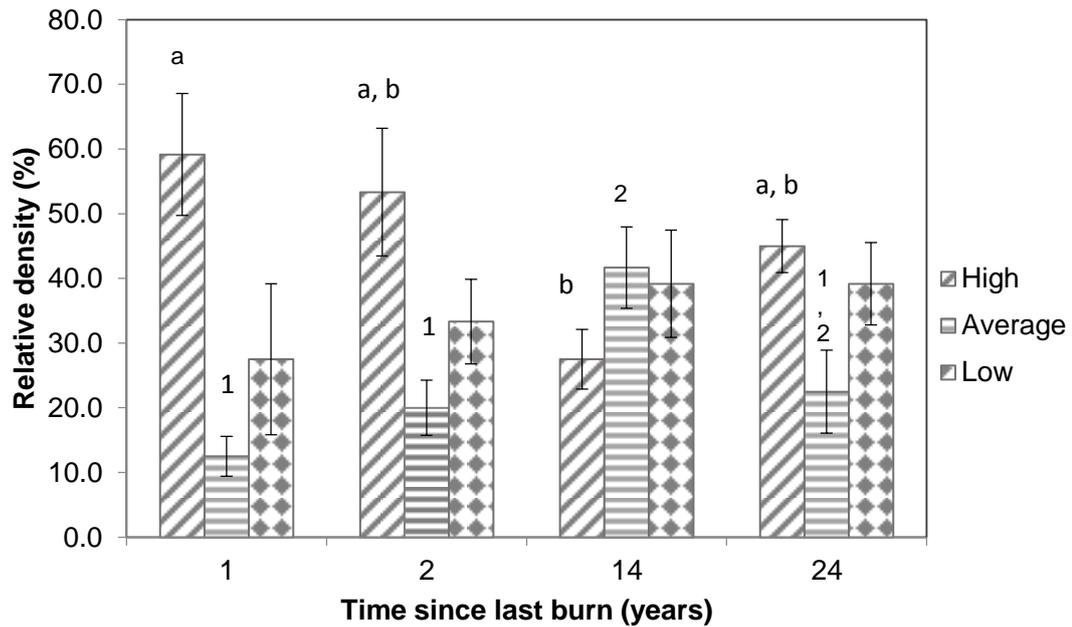


Figure 3.8: Relative density (%) in three grazing value categories in relation to time since last burn (years). Letters and numbers denote significant differences between treatments, while the bars show standard errors.

(d) Woody cover

Mean total woody cover significantly ($H= 19.698$, $df= 15$, $P< 0.05$, $n=6$) increased with time since last burn (Figure 3.9). Mean woody cover in the different height classes significantly differed except in <1 m ($H= 1.358$, $df= 15$, $P> 0.05$, $n=6$) (Figure 3.10a). In the 1 m– 2 m height class treatment 2 had a higher woody cover ($H= 15.091$, $df= 15$, $P< 0.05$, $n=6$) than all other treatments (Figure 3.10a). Treatment 24 had higher woody cover in 2 m- 3 m ($H= 19.579$, $df= 15$, $P< 0.05$, $n=6$) and 3 m- 4 m ($H= 20.249$, $df= 15$, $P< 0.05$, $n=6$) height classes than all other treatments (Figure 3.10b). In >4 m height class treatment 14 had higher woody cover ($H= 9.326$, $df= 15$, $P< 0.05$, $n=6$) than treatment 2 and treatment 24 (Figure 3.10b).

The woody species that contributed the most relative woody cover were *T. sericea* and *A. ataxacantha* (Table 3.3).

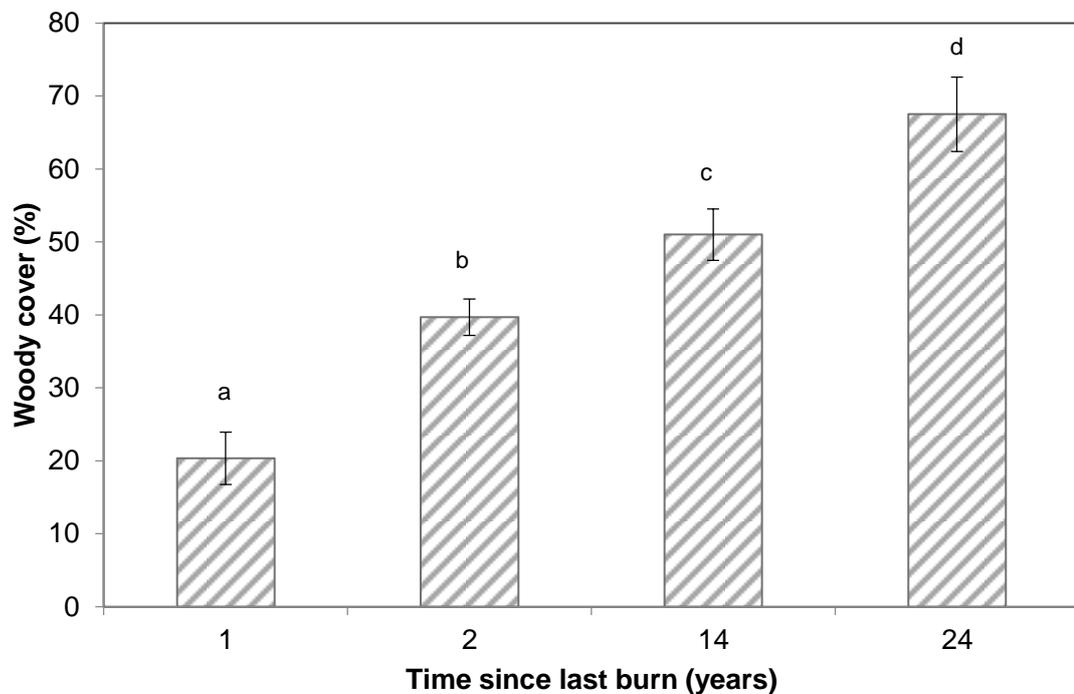


Figure 3.9: Total woody cover (%) in relation to time since last burn (years). Letters denote significant differences between treatments, while the bars show standard errors.

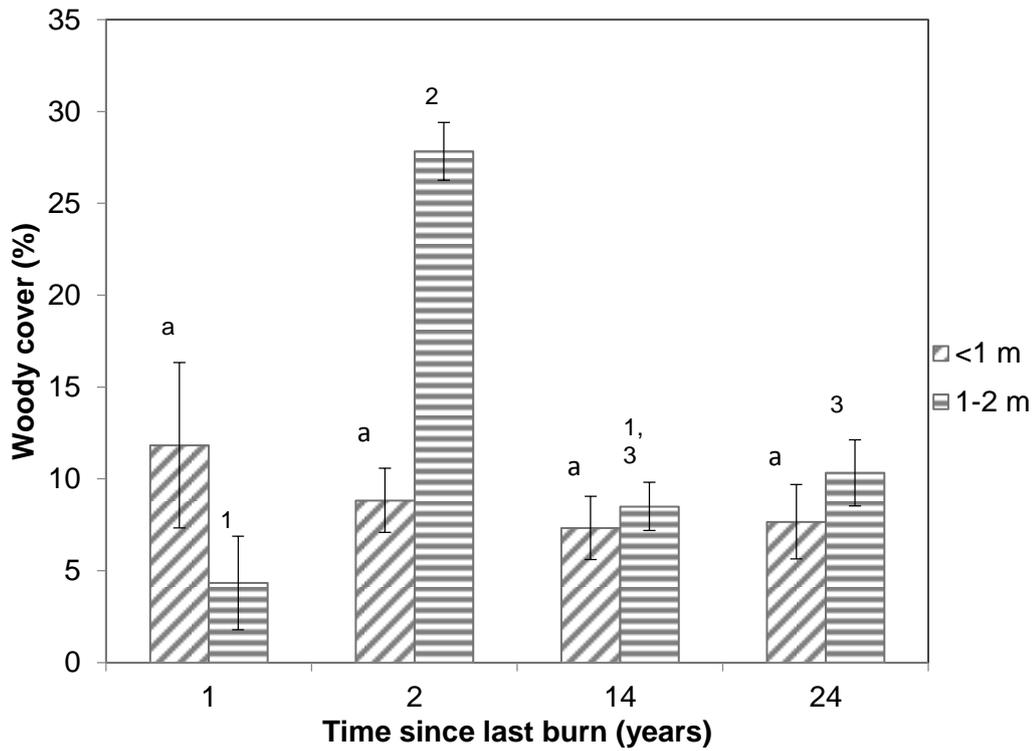


Figure 3.10a: Woody cover (%) in height classes of <1 m and 1 m- 2 m in relation to time since last burn (years). Letters and numbers denote significant differences between treatments, while the bars show standard errors.

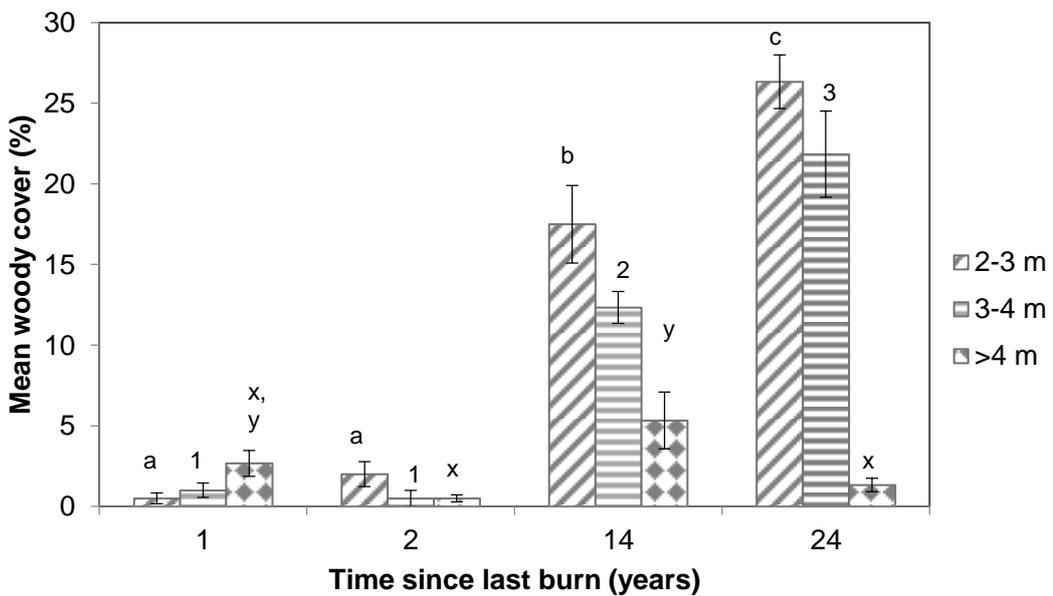


Figure 3.10b: Woody cover (%) in height classes 2 m-3 m, 3 m- 4 m, and >4 m in relation to time since last burn (years). Letters and numbers denote significant differences between treatments, while the bars show standard errors.

Table 3.3: Relative woody cover (%) of woody species in relation to time since last burn (years)

Woody species	Treatment			
	1	2	14	24
<i>A. ataxacantha</i>	16.3	13.8	20.9	23.6
<i>Acacia fleckii</i>	0	8.9	0	1.3
<i>Bauhinia petersiana</i>	1	2.9	4.1	11.9
<i>B. africana</i>	4	2	4.6	0.5
<i>Combretum apiculatum</i>	0	1.1	0.8	0
<i>C. collinum</i>	10.3	11	6.1	5
<i>C. psidioides</i>	10.5	7.1	15.2	3
<i>Croton gratissimus</i>	0	0	0	0.7
<i>Grewia avellana</i>	0	1.5	0	0
<i>G. flavescens</i>	1	0.8	2	1.6
<i>G. retinervis</i>	1.9	0.8	0	1
<i>O. pulchra</i>	1.4	2.2	2.2	5.2
<i>P. africanum</i>	11.2	0.4	2.5	0.7
<i>P. nelsii</i>	6.8	7	3.3	3.9
<i>Searsia tenuinervis</i>	0	0	1.6	0
<i>T. sericea</i>	34.9	40.5	35.9	41.6
<i>Z. mucronata</i>	0.6	0	0.7	0

(e) Species composition

i. Perennial grasses

The HCA separated the perennial grass species into 3 main clusters at about 25% similarity, with the recently burned treatments mainly in cluster 1, while the treatments burned more than 14 years ago grouped in cluster 3 (Figure 3.11).

Cluster 1 consists mainly of the recently burned treatment, and is characterised by transects with a higher relative density of *D. seriata* and relatively low densities of *Aristida stipitata* and *Stipagrostis uniplumis*.

Cluster 2 is a grouping of a few transects with a relatively low density of *D. seriata*

Cluster 3 mainly includes treatments burned 14 and 24 years ago, consisting of transects that have relatively high densities of *D. seriata* and *E. pallens*. *Triraphis schinzii* is only found in this cluster mainly in the treatment burned 14 years ago.

The NMS ordination revealed that organic carbon and nitrogen are the main environmental variables responsible for driving differences in relative density of different grass species in the different treatments (Figure 3.12).

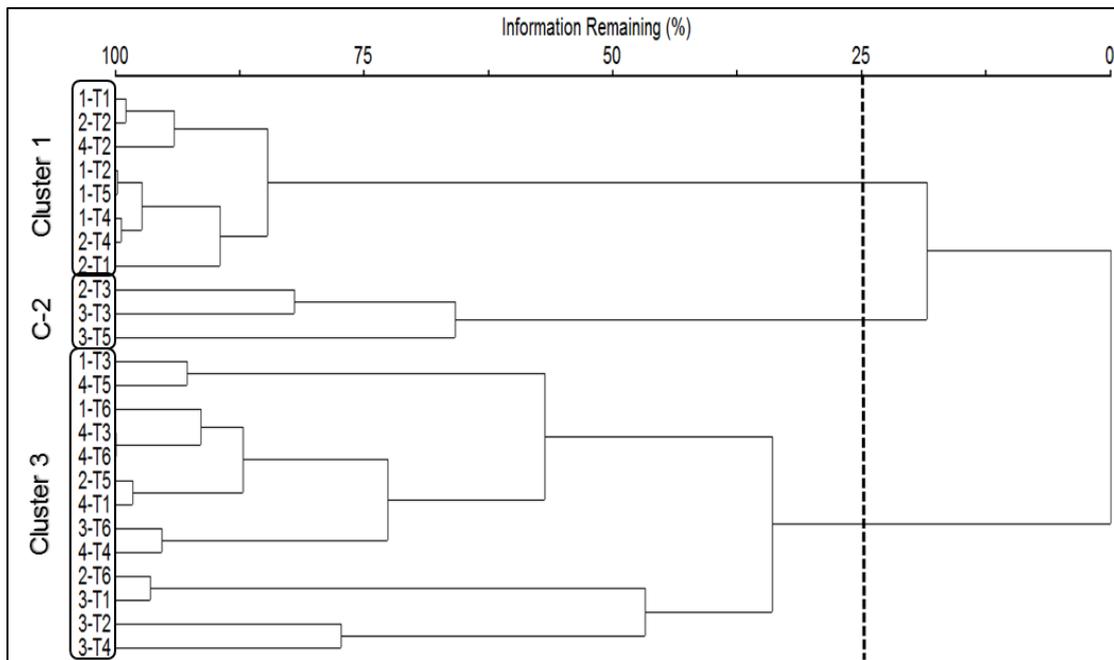


Figure 3.11: HCA dendrogram showing a classification of perennial grass species into 3 main clusters at 25% similarity (or 75% information remaining). The numbers denote the treatments: 1= 1, 2= 2, 3= 14 and 4= 24, while the letter & number represent the transect numbers, i.e. T1= transect 1.

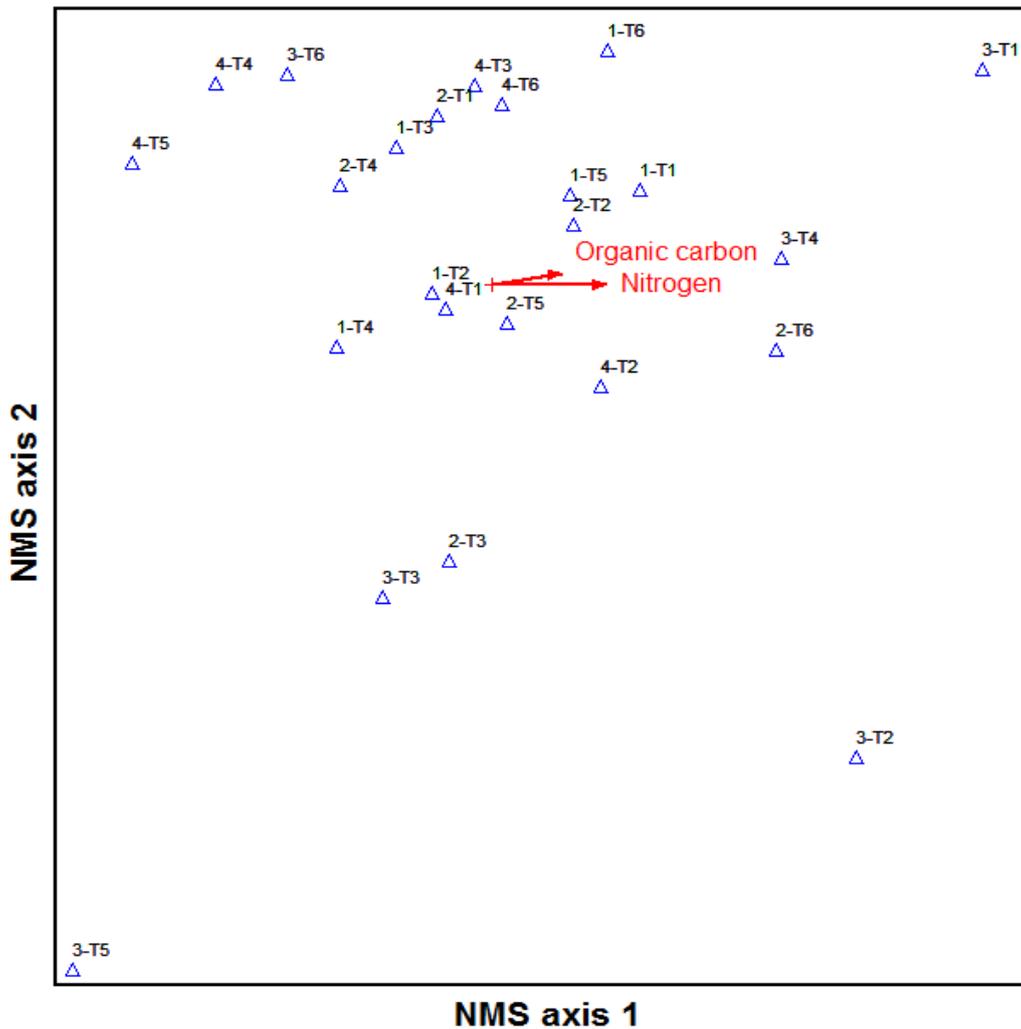


Figure 3.12: NMS joint plot for perennial grass species composition in relation to various environmental variables at r^2 cut off= 0.1. The numbers denote the treatments: 1= 1, 2= 2, 3= 14 and 4= 24, while the letter & number represent the transect numbers, i.e. T1= transect 1.

ii. Woody plant species

The HCA separated the woody species into 3 main clusters at about 30% similarity, but without any clear grouping of the different treatments (Figure 3.13).

Cluster 1 consists of transects that have relatively high woody cover of *Acacia ataxacantha* and *Terminalia sericea* but low cover of *Ochna pulchra*, *C. collinum* and *C. psidioides*. *C. gratissimus* was only found in this cluster.

Cluster 2 contains transects that have a relatively high woody cover of *C. collinum*, *C. psidioides* and *G. retinervis*. This cluster has the lowest woody cover of *T. sericea* and *Z. mucronata* is only found in this cluster.

Custer 3 has relatively low woody cover of *A. ataxacantha* and *C. collinum*, but with a relatively high woody cover of *B. petersiana*, *O. pulchra* and *T. sericea*.

The NMS ordination on the other hand revealed that fire history is not responsible for differences in relative woody cover of the different woody species in the different treatments but rather organic carbon, magnesium, calcium, potassium, nitrogen and phosphorus (Figure 3.14).

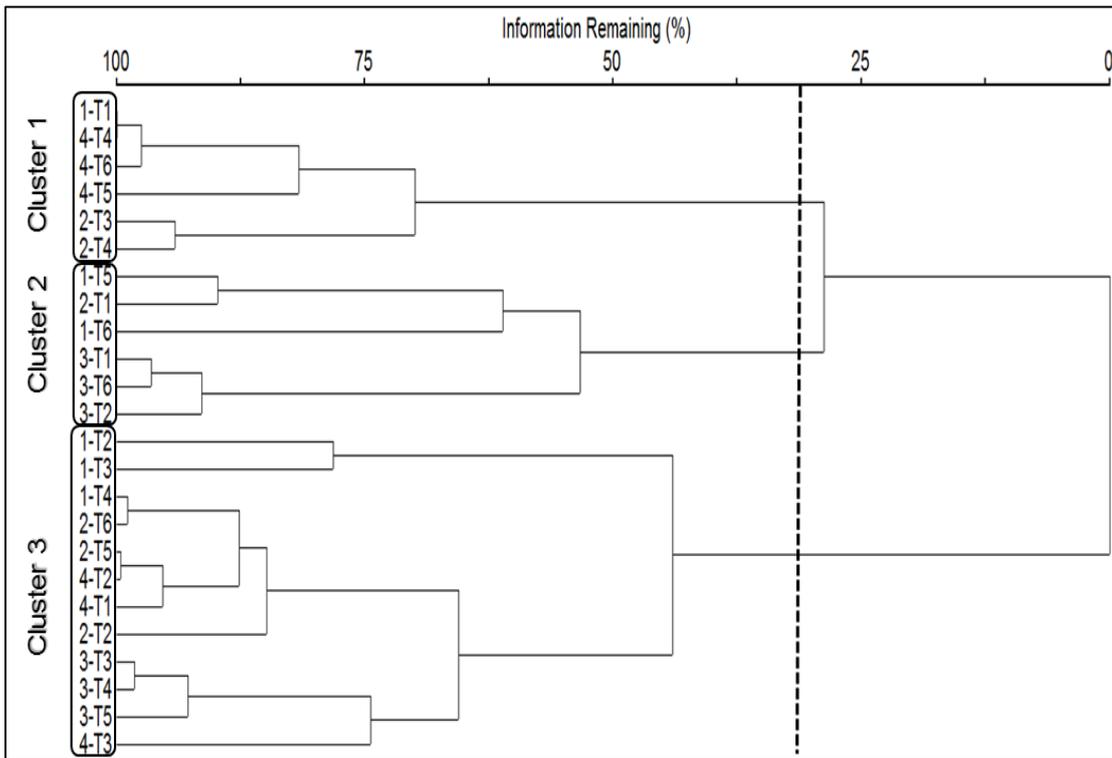


Figure 3.13: HCA dendrogram showing a classification of woody species into 3 main clusters at about 30% similarity (70% information remaining). The numbers denote the treatments: 1= 1, 2= 2, 3= 14 and 4= 24, while the letter & number represent the transect numbers, i.e. T1= transect 1.

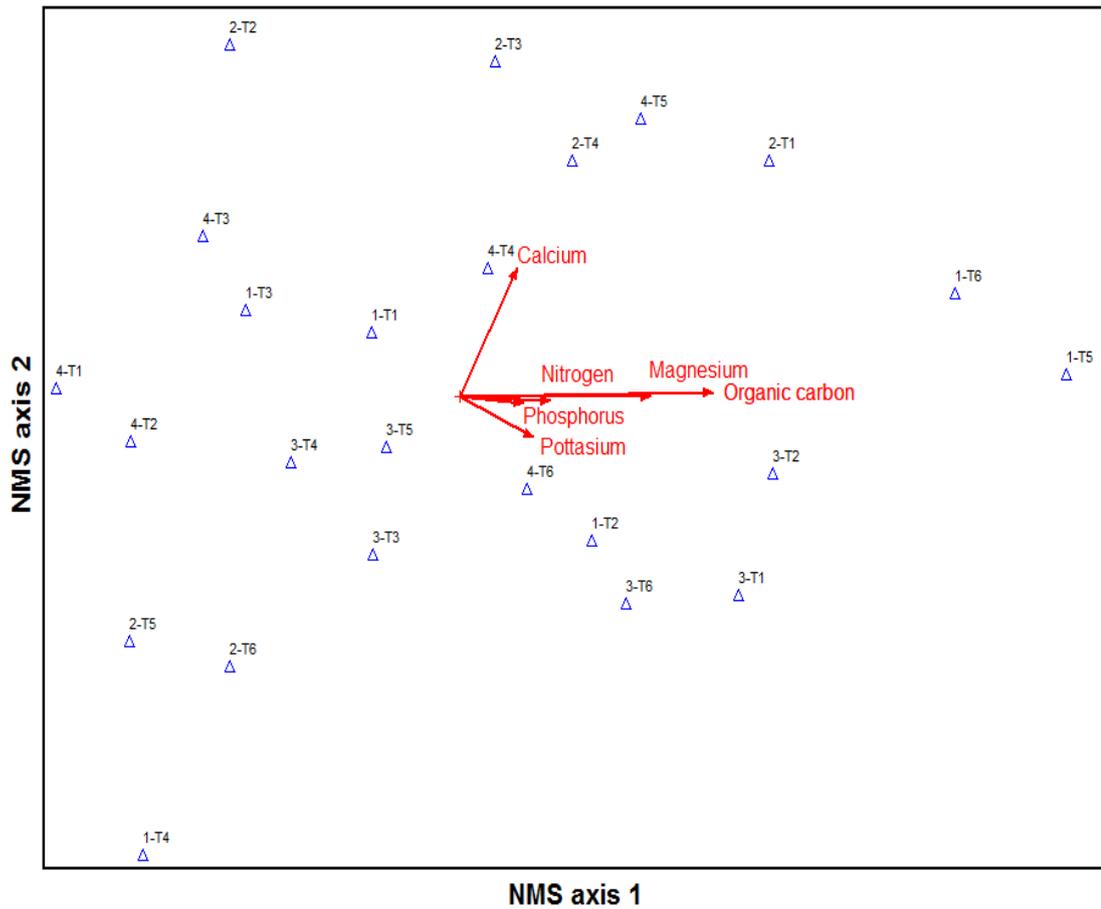


Figure 3.14: NMS joint plot for woody species composition in relation to various environmental variables at r^2 cut off= 0.1. The numbers denote the treatments: 1= 1, 2= 2, 3= 14 and 4= 24, while the letter & number represent the transect numbers, i.e. T1= transect 1.

3.6 Discussion

3.6.1 Effects of fire history on perennial grasses in a semi-arid savanna woodland

Fire is an important disturbance that affects perennial grasses (Zimmermann et al., 2010) either in a positive or negative way (Gul et al., 2014). Perennial grass density decreased with time since last burn being three times higher in the recently burned area (Figure 3.4). This is likely due to the removal of moribund grass, plant cover, shade, and reduced competition from established plants (Mapiye et al., 2008; Zimmermann et al., 2010; Nepolo & Mapaure, 2012; Gul et al., 2014) as well as reduction in canopy cover by fire (Holdo, 2007). This stimulates recruitment and regrowth of new grass shoots (Menke, 1992; van Oudtshoorn, 2004; Gul et al., 2014; Roodt, 2015). The new tillers regrow from existing grass base using their stored reserves when they are defoliated (du Toit et al., 2003; van Oudtshoorn, 2004; Nepolo & Mapaure, 2012; Roodt, 2015) through grazing or by fire. A species that does this in the study area is *D. seriata*, which is stoloniferous and roots at the nodes to form new tillers (Muller, 2007; Roodt, 2015). This tillering is an essential survival mechanism (Roodt, 2015) that enables perennial grasses to tolerate defoliation and maintain their status in the community (Gul et al., 2014). The new tillers in the recently burned treatment were regarded as individuals and this could have contributed greatly to the higher grass density.

Fire also appears to have changed the grass species composition towards more palatable species (Jankowitz, 1983; Trollope, 2003; De Klerk, 2004; Teie, 2009). A higher relative density of palatable grass species such as *D. seriata* was found in the treatments burned 1 and 2 years ago (Table 3.2; Figure 3.8) and this was also revealed by the HCA in cluster 1 (Figure 3.11). Generally, fires do not decrease palatable grasses but may significantly reduce unpalatable fibrous grass basal area as found in the similar *B. africana* savanna in Nylsvley (Scholes & Walker, 1993). The less palatable grass species also become more palatable after a fire as their crude protein content is higher (Mapiye et al., 2008; Mbatha & Ward, 2010; Gul et al., 2014) and are utilised as well (Gul et al., 2014; Uunona, 2014). Thus fire may improve range condition by increasing the abundance of valuable forage species (Trollope, 2004). The NMS ordination showed that organic carbon and nitrogen play a major role in this system (Figure 3.12). Thus, soil nutrients are also important determinants of grass community composition (Archibald et al, 2005; Kambatuku, Cramer & Ward, 2011).

The post-fire regrowth in the recently burned treatment is highly nutritious due to high crude protein content but is of little quantity (Gul et al., 2014). The recently burned treatment (488.4 kg/ ha) had about three and two times less grass biomass than treatments burned 2 (1425.7 kg/ ha) and 14 years (1030.2 kg/ ha) ago respectively (Figure 3.7). This could be due to fire burning away above-ground material of grasses causing a temporary decline in productivity

and a significant decrease in biomass of the grass layer (Scholes & Walker, 1993; van Langevelde et al., 2003; Goldammer & de Ronde, 2005; Mbatha & Ward, 2010; Zimmermann et al., 2010; Roodt, 2015). Grass biomass accumulation rate is usually noticeably lower in recently burned areas than on unburned sites for the first two months after fire, however above-ground productivity is almost double that on unburned sites and grass biomass is usually replenished at the end of one growing season after a fire (Scholes & Walker, 1993). The post-fire regrowth in the most recently burned treatment is more attractive to herbivores (Tainton, 1999; Tomor & Owen-Smith, 2002; Goldammer & de Ronde, 2005; Mills & Fey, 2005; Zimmerman et al., 2010; Roodt, 2015) that readily graze on this fresh grass shoots that are highly palatable and high in crude protein content (Erb, 1993; Scholes & Walker, 1993; Trollope, 2004; Goldammer & de Ronde, 2005; Mapiye et al., 2008), which reduces grass biomass. This was found to be the case in the study with the most recently burned treatment utilised up to four times more by herbivores than the other treatments (Uunona, 2014; Aindongo, 2015). The attraction of herbivores from unburned patches to recently burned patches by fire has been referred to as the “magnetic effect” by Archibald et al. (2005). Despite the treatment burned 2 years ago being the second most utilised (Uunona, 2014), it had the highest grass biomass. This could be attributed to the above mentioned reason of herbivores being attracted to the most recently burned area, thus giving the grasses a chance to grow and build-up biomass due to reduced grazing pressure and high productivity (Scholes & Walker, 1993; Zimmermann et al., 2010). This suggests that productivity of the recently burned areas if rested soon recovers and improves grass production (Scholes & Walker, 1993). This is supported by Archibald et al. (2005), who showed that burned areas attract animals off unburned grazed patches long enough for patches to recover full grass biomass in one growing season. This also explains why grass biomass was not significantly different between treatments 2 and 14. However, treatment 14 has grass biomass from many growing seasons which was mostly moribund, while treatment 2 only had grass biomass from two growing seasons.

The steady decline in perennial grass density with increasing time since last fire suggests that, with a longer period without fire, grasses accumulate dead plant material (unpalatable) (van Oudtshoorn, 2004; Roodt, 2015) and the build-up of competitive pressure between individuals becomes severe enough to lead to high mortality (Scholes & Walker, 1993; Zimmermann et al., 2010). Zimmermann et al. (2010) found that after 7 years without a fire in northern Etosha National Park sufficient standing dead biomass accumulated and competitive pressure induced high mortality rates (31%) of the perennial grass *S. uniplumis* var. *uniplumis*. The accumulated leaf biomass contributes to high fuel loads, which larger

grazers may utilise this high quantity but low quality forage (Tomor & Owen-Smith, 2002; Goldammer & de Ronde, 2005).

Besides being available forage for grazers, grass biomass is an important factor which influences fire behaviour, as fire intensity is positively related to the amount of fuel load (Scholes & Walker, 1993; Trollope et al., 2002; Sah, Ross, Snyder, Koptur & Cooley, 2006). The overall grass biomass in the study area is generally rather low compared to savannas with higher rainfall. Fuel loads tend to be sparser and more unevenly distributed in woodlands as compared to open savannas because of the influence of tree neighbourhoods on grass growth (Holdo, 2005). In broad-leaved savannas such as Kalahari sand woodlands, trees are better competitors than the grasses, and thus in absence of tree-thinning disturbances, grass cover is sparse (Knoop & Walker, 1985 in Holdo, 2005). In addition, *T. sericea*, a species considered to be an encroacher in the study area, could be a significant competitor with the grasses, due to its shallow root system (Hipondoka & Versfeld, 2006; Lutibezi, 2016). It forms dense thickets and acts like a weed, and may prevent the growth of grasses (Hipondoka & Versfeld, 2006).

3.6.2 Effects of fire history on woody plants in a semi-arid savanna woodland

Time since last burn did not significantly affect total woody density (Figure 3.5). Alone, this would suggest that fire in this semi-arid savanna woodland is not adequate to reduce woody plant density and maintain an open savanna. However, other factors such as fire intensity should be taken into account. While fire intensity is a crucial, it is important to highlight that there have been very little efforts made in African savannas and grasslands to quantitatively measure fire intensity and relate it to how herbaceous and woody components respond to it in terms of mortality (Trollope, 2003; Goldammer & de Ronde, 2004).

Some of the efforts made to assess effects of fire intensity on woody vegetation have yielded the following results: Fire intensity strongly affects tree mortality in the KNP (Govender et al., 2006), with high intensity fires reducing woody density (du Toit et al., 2003; Rains, 1963 & Kennan, 1972 in Scholes & Walker, 1993). Fire intensity is linearly related to the amount of grass biomass (Higgins et al., 2000; van Langevelde et al., 2003; Holdo, 2005; Sah et al., 2006) which is dependent on rainfall (Scholes & Walker, 1993) and the impact of fire on woody plants is also linearly related to how intense the fire is (van Langevelde et al., 2003). These effects are more prevalent in higher rainfall areas such as the north-eastern parts of Namibia (Mendelsohn & el Obeid, 2005). Thus, high intensity fires are likely to be rare in the study area due to lower rainfall and thus generally low fuel loads (Figure 3.7), with the highest amount of grass biomass being 1425 kg/ ha, despite a good rainfall season with a total of 913.9 mm (2013-2014 rainfall period) (Appendix 2). The grass biomass could also be

significantly reduced through utilisation by grazing herbivores, and thus less intense fires (du Toit et al., 2003; van Langevelde et al., 2003; Archibald et al., 2005). However, this was not the case in the study area as the treatment burned 2 years ago had the highest grass biomass despite a high utilisation (Uunona, 2014), suggesting a positive effect of fire on grass productivity. A similar plateau nearby (“Omuverumwe”) with the same vegetation type as the study area but that does not have large herbivores due to its inaccessibility seems to have a different vegetation structure. Preliminary observations suggest that it has very few saplings, taller woody plants and overall lower woody density and higher grass biomass than the study area. Self-thinning could be one possible factor that has over time led to Omuverumwe having taller but less dense woody plants (Scholes & Walker, 1993). However, the possible key difference resulting in these differences between the two plateaus is large mammal presence; since there is no utilisation by large mammals on Omuverumwe the fuel loads are higher and thus more intense fires occur that may have reduced woody density by affecting tree recruitment (Nepolo & Mapaure, 2012). The amount of fuel load in the study area from a classification by Trollope & Potgieter (1985) in Trollope (2003) would result in a cool to moderately hot fire intensity that is not intense enough to kill woody plants (Trollope, 2003). In this system, therefore, fire is likely to have changed the structure.

Although, total woody density did not differ, the distribution of woody density in the different height classes was significantly different among treatments (Figures 3.6a, 3.6b & 3.6c). Recent fires caused top-kill of woody stems decreasing their height to “browsable” heights (Trollope, 2003; Bothma & du Toit, 2005; Joubert et al., 2012); the resulting resprouts are more accessible and more nutritious for browsers (Scholes & Walker, 1993). The effects of fire are more pronounced in the smaller size classes, as their bark is not thick enough to insulate them against the heat and because their crowns are within the flame zone (Holdo, 2005; Burke, 2006). Therefore, without fires over the years woody plants are able to grow taller and escape the fire trap (Smit et al., 2010). These taller mature trees with a thicker bark that protects the main stem and buds held above the flame zone are less affected by fire (Tainton, 1999; Accatino et al., 2010). This is evident in the study area as they are found in low densities in the recently burned treatments (Figure 3.6c).

A trend in mean total woody cover was observed with woody cover increasing with time since last burn (Figure 3.9). This could be attributed to reduced woody cover through top-kill by fire in the recently burned areas (du Toit et al., 2003; Trollope, 2003; Holdo, 2005; Smit et al., 2016) and as a result a more open area dominated by woody plants < 2 m that contribute to woody cover. In the absence of fire over the years woody plants grow taller and their canopies become bigger resulting in higher woody cover (Accatino et al., 2010; Smit et al., 2010) and consequently a more closed woodland with woody plants mainly > 2 m (Figure

3.10). The increase in woody cover is thus not because of an increase in density but rather an increase in the size of individual canopies free of fire.

The dominant woody species in the study area found were *T. sericea* and *A. ataxacantha* (Table 3.4). The dominance of a species in an area is mainly due to its growth rate, competitive ability, resistance or tolerance to disturbances or a combination thereof etc. *T. sericea* for instance is a species that occurs predominantly on deep sandy soils (Mendelsohn & el Obeid, 2005; Mannheimer & Curtis, 2009). It has the tendency to deploy its roots near the surface, enabling it to compete for available water and nutrients with other shallow rooted plants such as grasses (Hipondoka & Versfeld, 2006). *T. sericea* is also fire-resistant (Holdo, 2006) and when damaged by fire or cutting it is known to coppice vigorously (Mendelsohn & el Obeid, 2005; Moyo, 2013). It forms dense thickets (Moyo, 2013) and is considered to be an encroaching species in the study area (Lutibezi, 2016).

The HCA separated the woody species into three main clusters but without any grouping in relation to time since last burn (Figure 3.13). The NMS ordination results also revealed that soil nutrients other than fire are the driving factor of woody species composition (Figure 13.14). Fire tolerance thresholds of various species and development stage of individual plants when a fire occurs are the two most important aspects determining the long-term impacts of fire on species composition (Burke, 2006). As discussed earlier, savanna woody plants are well adapted to fire and resprout after being top-killed, persisting as gullivers. Drastic changes in vegetation species composition is also more likely to occur in mesic savannas (O'Connor, 1985 in Gandiwa, 2011). Besides moisture availability, soil nutrients in savanna systems are the main driving factor for vegetation distributions (Scholes & Walker, 1993). While this savanna is dystrophic, animal behaviour and woody plants may influence nutrient distributions, which may in turn influence vegetation distribution and growth (Scholes & Walker, 1993; Holdo & Mack, 2014). When animals seek for shade under trees they may concentrate nutrients under canopies, creating "nutrient hotspots" (Holdo & Mack, 2014). In addition, trees can also redistribute nutrients and water into the sub-canopy through hydraulic lift by pumping these from areas beyond their canopies and from deeper soils (Scholes & Walker, 1993; Holdo & Mack, 2014).

3.7 Conclusions

The effects of fire history in this semi-arid savanna woodland are a temporary improvement of the forage quality with an increase in grass density, a slight increase in more palatable grass species and overall palatability. The post-fire regrowth attracts animals to the most recently burned areas, which allows other burned sites such as the treatment burned 2 years ago to recover lost grass biomass. In the absence of fire for many years, perennial grasses

grow bigger and accumulate moribund material. This low quality forage is rarely utilised except by large herbivores that graze it to increase their intake.

Fire history had no significant effect on vegetation species composition and overall woody density. However, fire acted mainly on the structure, maintaining an open savanna through top-kill which decreases plant height and woody canopy cover. Without fire, woody plants grow taller beyond the fire trap and their canopies increase resulting in more closed savanna woodland.

CHAPTER 4

EFFECTS OF FROST ON VEGETATION STRUCTURE AND SPECIES COMPOSITION IN A SEMI-ARID SAVANNA WOODLAND

4.1 Introduction

Frost is generally overlooked when studying factors that affect vegetation but could be as important as fire (Holdo, 2006). Frost refers to the formation of ice crystals on surfaces, either by freezing of dew or a phase change from water vapour to ice (Snyder & de Melo-Abreu, 2005). It occurs when the air temperature is 0 °C or less (Snyder & de Melo-Abreu, 2005). Frost can arise in two ways; advective frost occurs when a cold front sweeps into an area replacing the warmer air. This occurs during cloudy conditions, with moderate to strong winds, low humidity and no temperature inversion (Snyder & de Melo-Abreu, 2005). Radiation frost occurs under clear skies, with very little wind, low dew-point temperatures, temperature inversion and air temperatures that go below 0 °C during the night but are above 0 °C during the day (de Long, 2001; Snyder & de Melo-Abreu, 2005). This occurs when radiant heat from the earth rise to upper layers of the atmosphere and the absence of wind prevents the mixing of this air with cold air, creating an inversion layer (Reddick, undated). The heavier cold air settles near the ground while the warm air lies above it (de Long, 2001; Mendelsohn & el Obeid, 2005; Reddick, undated). Radiation frost occurs in Namibia, including savanna woodlands. In the WPP it mostly occurs in low-lying areas (Mendelsohn & el Obeid, 2005) referred to as “interdunes” or loosely termed as “frost pockets” (de Long, 2001; Reddick, undated) where cold air settles in winter. Frost forms as a layer of ice on the soil surface when the air temperatures drop below 0 °C and the dew point is close to the ground surface (Whitecross et al., 2012). In Namibia frost occurrence is more prevalent in the central eastern regions of the country that experience on average more than 30 days of frost, while elsewhere such as WPP the average number of days with frost is considered to be 6-10 (Mendelsohn & el Obeid, 2005) (Figure 4.1).

Frost events are major environmental disturbances responsible for losses and limiting the distribution of vegetation (Whitecross et al., 2012). Direct damage to plants by frost occurs when ice crystals form inside the protoplasm of cells (intracellular freezing that is associated with rapid cooling) (Snyder & de Melo-Abreu, 2005). Indirect damage occurs when ice forms inside the plants but outside the cells (extracellular freezing) and is the most common type that occurs in nature (Snyder & de Melo-Abreu, 2005). Thus it is ice formation that leads to severe damage or the death of plant tissues (Snyder & de Melo-Abreu, 2005; Whitecross et al., 2012). It exerts direct effects on plant roots by limiting available moisture and causes damage to above ground parts of plants (Benninghoff, 1952). The softest tissues like leaves

and new shoots are injured first and the tougher stem tissue and buds down from the tips are less damaged (Reddick, undated). The intensity of damage is dependent on how cold and how quickly temperatures drop below freezing point and how long this lasts (Snyder & de Melo-Abreu, 2005; Reddick, undated). In the study area, frost top-kills aerial parts of woody plants in the interdune areas, which resprout from the base during the growing season (personal observations).

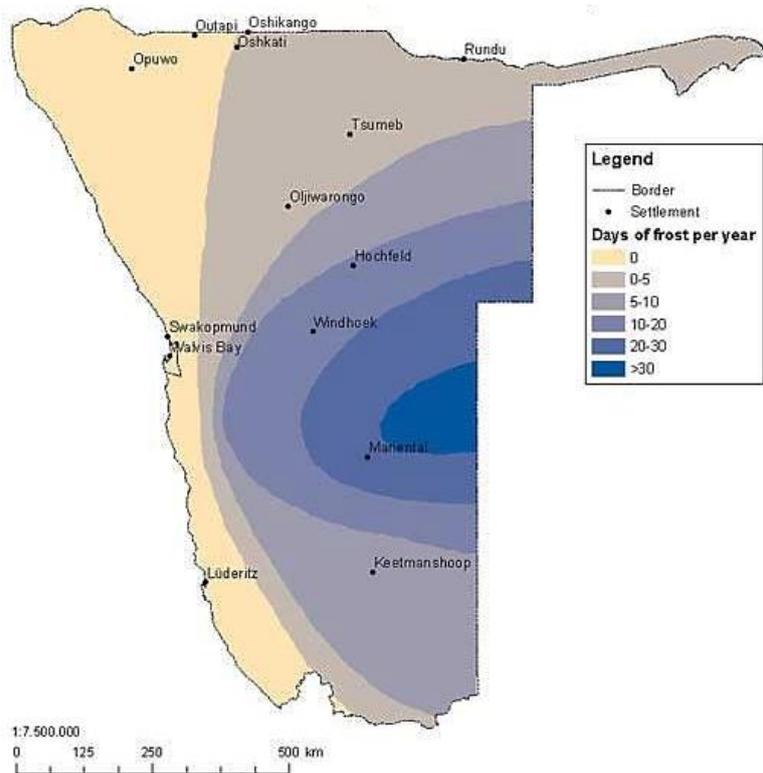


Figure 4.1: Average number of frost days (ranging from 0 to more than 30 days) in different parts of Namibia (Source: Mendelsohn, Jarvis, Roberts, & Robertson, 2002)

4.2 Literature review

Very few studies have been done that focus on, or include the effects of frost on vegetation in the southern African savannas (Whitecross et al., 2012). Frost could be an important disturbance which may be a key determinant of structure and species composition in some Southern African savannas either alone or in conjunction with fire (Holdo, 2005; Whitecross et al., 2012). Frost events vary in impact depending on the plants' ability to withstand cold temperatures as well as the duration of the disturbance (Whitecross et al., 2012). Frost can slow the growth of trees (Mendelsohn & el Obeid, 2005).

To survive frost damage, some plants have evolved adaptive mechanisms. These mechanisms include plant tissues having anti-freeze proteins that aid in lowering the freezing

point of that material. However this mechanism generally seems to be absent in Southern African savanna species (Whitecross et al., 2012). In Southern African savannas, most plant species tolerate frost conditions by being deciduous and shedding their leaves before temperatures become cold enough for frost events to occur (Whitecross et al., 2012). Another survival mechanism is resprouting, a life-history strategy for trees occurring in low rainfall and poor nutrient soils which is an alternative to increasing seedling recruitment (Whitecross et al., 2012). However, plant survival may depend on the growth stage and development of plants at the time of disturbance (Reddick, undated). Generally, older more mature plants are able to tolerate freezing temperatures better than juvenile plants (Mendelsohn & el Obeid, 2005; Reddick, undated) and usually resprout from epicormic buds (means by which woody plants regrow after coppicing) after being top-killed by frost (Rushworth, 1975 in Holdo, 2006). Those plants that cannot withstand frost simply do not occur in frost-prone areas (Mendelsohn & el Obeid, 2005).

The results of a study by Whitecross et al. (2012) on whether freeze events create a demographic bottleneck for *Colophospermum mopane* found that the most severe freeze conditions occurred at the lower elevations causing the most severe damage to trees occurring there. They also assessed the damage on *C. mopane* at different heights on individual plants and found that the most severe damage occurred between the heights of 1.5 m and 2.5 m, while trees above 4 m (threshold) did not experience more than 75% top-kill from frost (freeze-damage). The study also found that *B. africana* and *Combretum* spp were negatively affected by frost events in southern African savannas (Whitecross et al., 2012).

Frost damaged trees are more prone to being top-killed during a fire than frost undamaged trees (Holdo, 2005). Fire can interact with frost to produce high levels of above-ground mortality (Holdo, 2005). In addition, frost kills plant tissues, increasing the amount and height of above ground fuel load, which in turn increases the intensity of fire causing a higher rate of mortality than is expected from the effects of fire alone (Rushworth, 1975 and Chlides & Walker, 1987 in Holdo, 2006). Frost events also expose new growth to higher risks of damage (Whitecross et al., 2012).

4.3 Key research objectives, questions and hypotheses

The specific objectives of the study were to compare the effects of frost occurrence at the Waterberg Plateau Park on the following:

- (a) vegetation density
- (b) grass biomass

- (c) grazing value of perennial grasses
- (d) woody cover and
- (e) species composition

The study sought to answer the following questions: How does frost occurrence affect the following:

- (a) vegetation density
- (b) grass biomass
- (c) grazing value of perennial grasses
- (d) woody cover and
- (e) species composition?

The research hypotheses of the study were:

- (a) Perennial grass density is not affected by frost occurrence as it is likely to be dormant when frost occurs. Woody density increases in the absence of severe disturbances such as frequent frost occurrence.
- (b) Grass biomass will not be significantly different between the interdune and dune areas, as frost does not occur in the growing season but occurs when the above-ground grass matter is dormant.
- (c) Relative density of palatable and unpalatable perennial grass species will not differ between the dune and interdune areas as frost occurrence does not affect grasses.
- (d) Woody canopy cover is negatively affected by frost occurrence and increases in the absence of frost occurrence. Woody cover contributed by plants <3 m will be significantly higher in the “interdune” areas compared to the dune areas as frost top-kills woody plants keeping them short. Whereas, woody plants >3 m will contribute significantly higher to woody cover on the dune where frost occurrence is not as frequent.
- (e) Frost occurrence indirectly influences relative density of grass species through increased light penetration but negatively affects relative cover of woody species composition through top-kill. Frost tolerant vegetation species will dominate in the interdune areas, while vegetation species that are less tolerant of severe frost will occur predominantly on the dune areas.

4.4 Data collection

4.4.1 Surveyed treatments

The study was carried in a treatment with a clear dune system with the same fire history (Figure 3.1; Plate 4.1-4.2).

Table 4.1: The surveyed treatments with frost occurrence, mean fire return interval and time since they were last burned (Joubert, 2013: unpublished data)

Treatment and position	Mean fire return interval (years)	Time since last burn (years)
5- interdune	12.3	24
5- dune	12.3	24

Note: The number of years for time since last burn was at the time of data collection in 2015



Plate 4.1: A dune area burned 24 years ago (Image: N. Uunona)



Plate 4.2: An interdune area burned 24 years ago (Image: N. Uunona)

4.4.2 Sampling methods

In each of the treatments twelve 100 m line transects were randomly selected. Along each transect three points were surveyed using the same methods as in chapter 3, sub-section 3.1.4.2. The area is shown in Figure 3.1 (labelled as 5) in chapter 3, subsection 3.1.4.1. In addition to these, winter temperatures in the interdune areas and dune areas were recorded with seven temperature sensors (Thermadata loggers: model TD with internal sensors, Keison products, England) in each treatment placed along randomly selected transects at the second sampling point. They were tied onto the stem of the nearest woody plant to the point 2 cm above the ground. The Thermadata loggers were set to record the temperature every 45 minutes during the winter period (May to August).

Soil samples were also collected at the second sampling point from all transects in the interdune and dune areas. The following were analysed from the various properties tested: organic matter, phosphorus, potassium, calcium, magnesium, sodium, and nitrogen as well as percentage clay. The analyses were done at the soil laboratory at the Ministry of Agriculture, Water and Forestry.

4.4.3 Data analysis

The statistical software package STATISTICA 12 (StatSoft, 2002) was used to run all statistical tests. The Kolmogorov-Smirnov test was used to see if data were normally distributed. If the data were normally distributed the t-Test was used and if not the equivalent non-parametric Mann-Whitney test was used to test for significant differences.

(a) Temperature assessment

Upon collection of the Thermadata loggers 3 were found on the ground, 2 in the interdune areas and the other on the dune area. These sensors were excluded from the analysis since ground temperatures were not guaranteed to be comparable. Only the temperatures ≤ 0 °C were considered. The number of days with temperatures ≤ 0 °C, the mean temperatures ≤ 0 °C and the minimum temperature per transect were calculated. The coldest temperatures in both treatments were also highlighted. To test for significant differences between the interdune and dune areas, a t-Test: independent by groups was used.

(b) Vegetation density

The density of the perennial grasses and woody plants was calculated using the following formula:

$$\text{Density} = 1 / (\text{average distance in meters})^2 \text{ (Mitchell, 2007)}$$

The density was calculated as individuals per hectare for each treatment. Woody plant density was calculated per height class as well as mean total woody density. To test for significant difference between the interdune and dune area, a t-Test: independent by groups was used.

(c) Grass biomass

The VOR method readings and the dry weight were plotted as a scatter plot and a regression line was obtained from this (Appendix). The following regression equation was used to convert the VOR results into grass biomass:

$$y = 65.026x + 20.123, \text{ with } R^2 = 0.558$$

Where y= biomass in grams, x= VORs as number of ring bands obstructed by grass

The mean grass biomass per transect in all the treatments was calculated. To test for significant difference between the interdune and dune area, a t-Test: independent by groups was used.

(d) Grazing value of perennial grass species

The different grass species were classified into the following grazing value categories: High grazing value, average grazing value and low grazing value using an index from Grasses of Namibia by Muller (2007) (Appendix 5). The mean for each grazing value category in all treatments was calculated. To test for significant difference between the interdune and dune area, a t-Test: independent by groups was used. The relative density of the perennial grasses was calculated using the following formula:

$$\text{Relative density} = (n_i / \sum n) * 100$$

Where n_i = number of individuals of each species and $\sum n$ = total number of all individuals

(e) Woody cover

The number of hits obtained in the field using the Bitterlich gauge with dimensions $l = 75$ cm and $b = 33.5$ cm were converted to percentages by multiplying them with 5. The mean woody cover was calculated per height class in each transect as well as mean total woody cover. To test for significant difference between the interdune and dune area, a t-Test: independent by groups was used.

(f) Species composition

The same procedure as explained in chapter 3, subsection 3.1.4.3 was used. However, environmental variables used in the ordination were: frost occurrence and the following soil properties: clay %, organic carbon, phosphorus, potassium, calcium, magnesium, sodium, and nitrogen.

4.5 Results

(a) Temperature assessment

As expected significantly lower average temperatures ≤ 0 °C and average minimum temperatures ≤ 0 °C were recorded in the interdune areas. The coldest temperatures and the number of days with temperatures ≤ 0 °C were also recorded in the interdune areas. Surprisingly, the dune areas also experience very cold temperatures (Table 4.2).

Table 4.2: Comparison of temperature parameters between the interdune and dune areas

Temperature parameters	Interdune	Dune	Statistical results
Number of days with ≤ 0 °C	89 days	80 days	–
Average temperature ≤ 0 °C	-3.87 °C \pm 0.273 °C	-3.02 °C \pm 0.123 °C	T= 4.490, df= 9, P< 0.05
Average minimum temperature	-14.3 °C \pm 1.133 °C	-10.5 °C \pm 0.714 °C	T= 4.795, df= 9, P< 0.05
Coldest temperature	-14.6 °C	-13.6 °C	–

(b) Soil properties

There were no significant differences in any of the soil properties between the interdune and dune areas (Table 4.3).

Table 4.3. Comparison of soil properties between the interdune and dune areas

Soil properties	Interdunes	Dunes	Significance
Organic carbon (%)	0.411 ± 0.05	0.467 ± 0.061	T= -0.678, df= 22, P> 0.05
Phosphorous (ppm)	4.975 ± 0.383	3.75 ± 0.560	T= 1.805, df= 22, P> 0.05
Potassium (ppm)	16.083 ± 1.856	16.417 ± 2.518	T= -0.107, df= 22, P> 0.05
Calcium (ppm)	80.333 ± 11.867	149.417 ± 57.965	T= -1.168, df= 22, P> 0.05

Soil properties	Interdunes	Dunes	Significance
Magnesium (ppm)	21.583 ± 2.627	26 ± 4.069	T= -0.912, df= 22, P> 0.05
Sodium (ppm)	19.083 ± 7.167	16.667 ± 6.125	T= 0.256, df= 22, P> 0.05
Nitrogen (%)	2.575 ± 0.190	2.533 ± 0.196	T= -0.152, df= 22, P> 0.05
Clay (%)	0.057 ± 0.006	0.058 ± 0.003	T= 0.153, df= 22, P> 0.05

(c) Vegetation density

i. Perennial grass density

The interdune areas had twice (T= 3.404, df= 22, P< 0.05, n=12) as much mean perennial grass density than the dune areas (Figure 4.2).

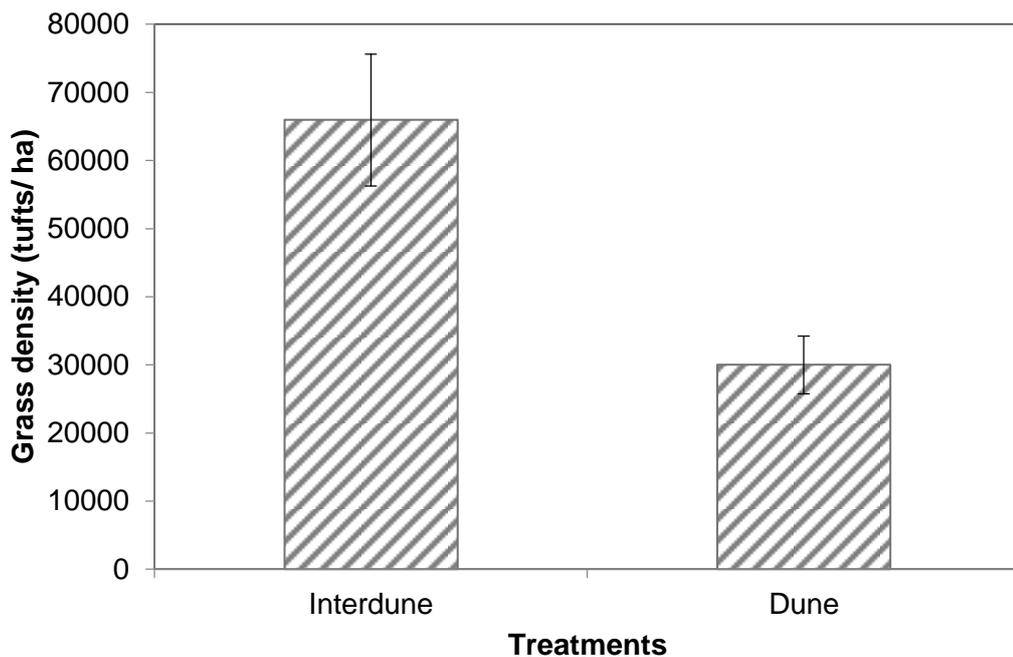


Figure 4.2: Perennial grass density (grass tufts/ ha) in relation to frost occurrence

ii. Woody density

Mean total woody density was not significantly (T= 2.002, df= 22, P= 0.058, n=12) different between the interdune and dune areas, although the latter had a mean density three times more (Figure 4.3). This was also the case for the < 1 m height class (T= 2.021, df= 22, P= 0.056, n=12), with no significant results being likely due to high variation. Mean woody density in the different height classes was only

significantly different ($T = -3.719$, $df = 22$, $P < 0.05$, $n = 12$) in the > 4 m height class, with the dune areas having about three times more woody individuals/ ha in this height class (Figure 4.4b).

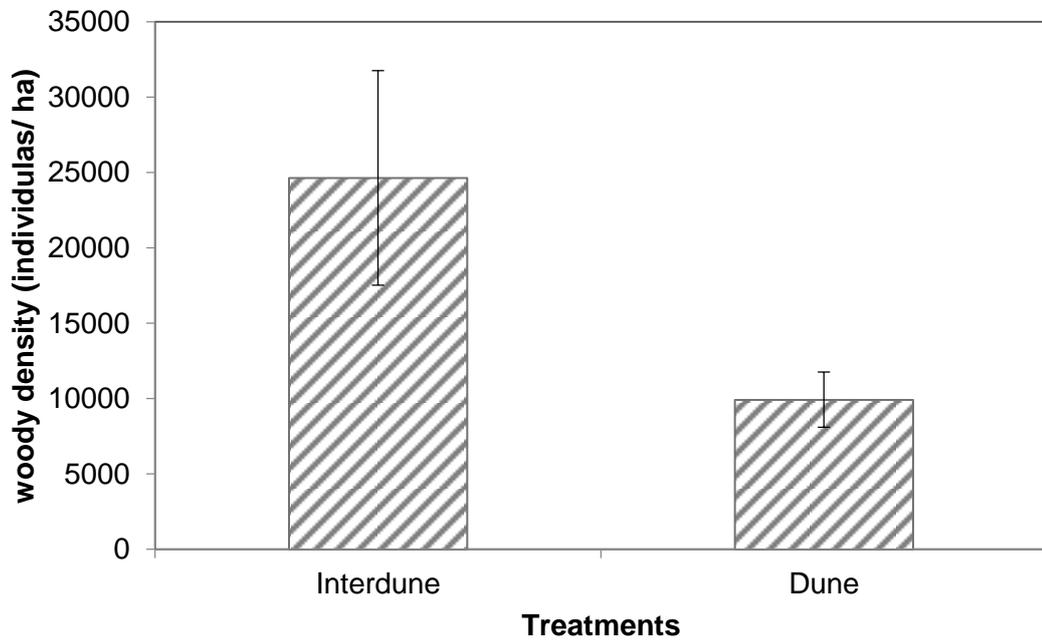


Figure 4.3: Total woody density (individuals/ ha) in relation to frost occurrence

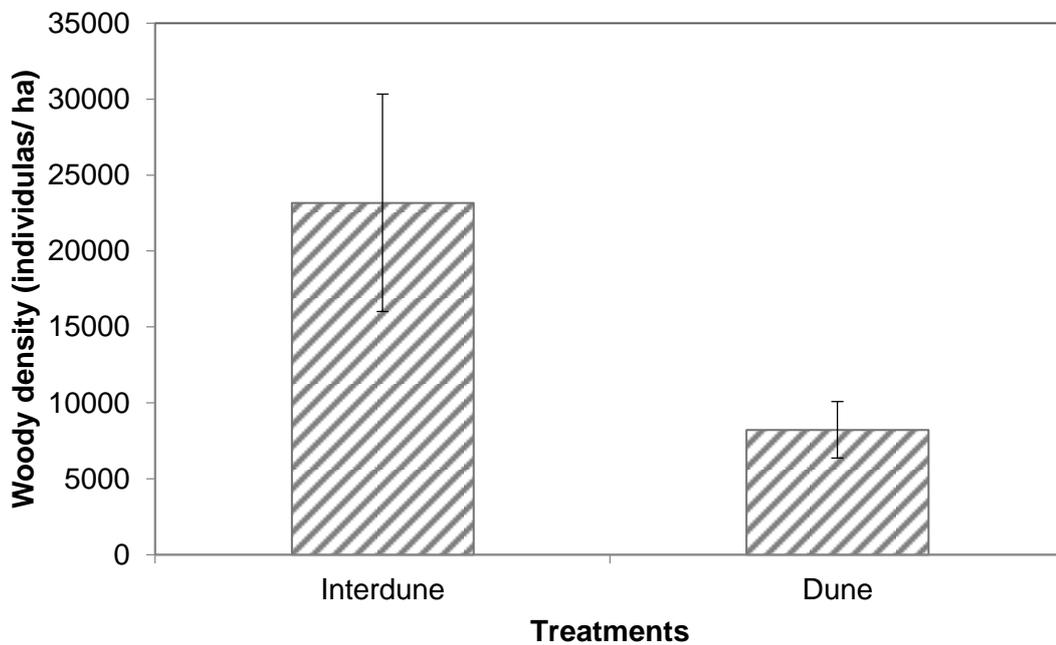


Figure 4.4a: Woody density (individuals/ ha) in the height class < 1 m in relation to frost occurrence

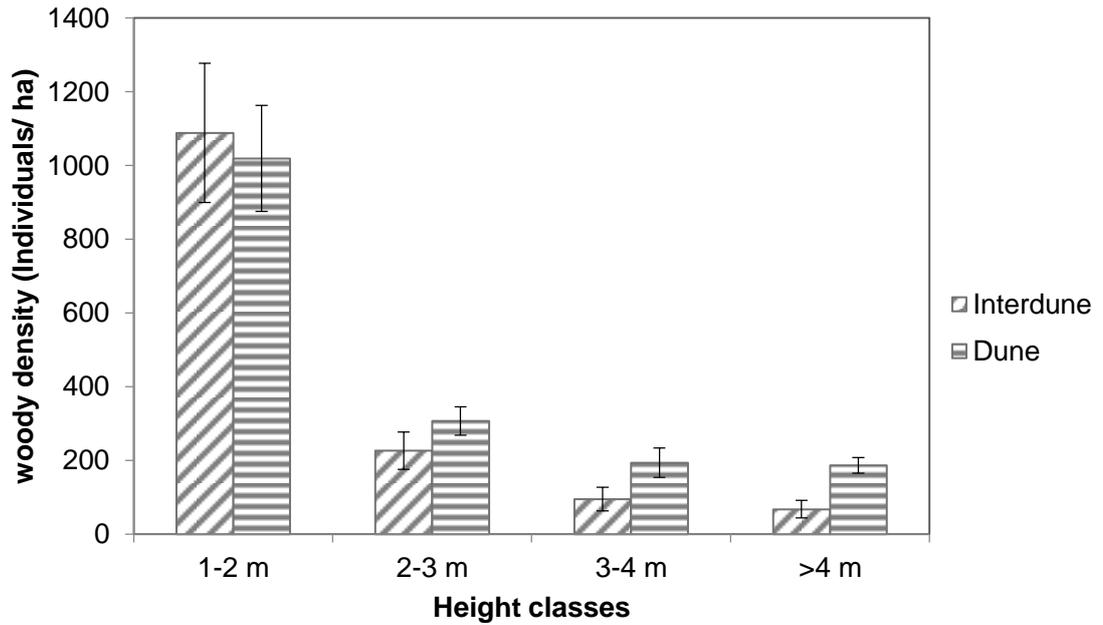


Figure 4.4b: Woody density (individuals/ ha) in the height classes 1 m to > 4 m in relation to frost occurrence

(d) Grass biomass

Grass biomass was generally low (652.7 kg/ ha in the interdune areas and 557.9 kg/ ha in the dune areas) (Figure 4.5) and did not differ significantly ($T = 0.514$, $df = 22$, $P > 0.05$, $n = 12$).

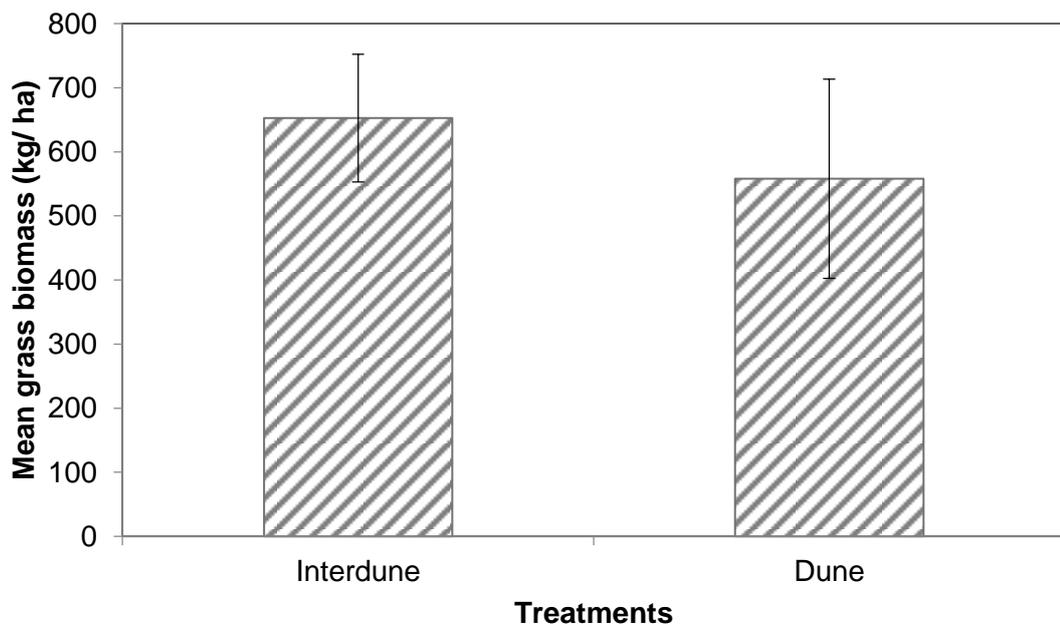


Figure 4.5: Grass biomass (kg/ ha) in relation to frost occurrence

(e) Grazing value of perennial grasses

The interdune areas had significantly higher ($T = -2.665$, $df = 22$, $P < 0.05$, $n = 12$) relative density of high grazing value perennial grass species and significantly ($T = 2.904$, $df = 22$, $P < 0.05$, $n = 12$) lower relative density of low grazing value perennial grasses. The perennial grasses with average grazing value did not significantly differ ($T = 0.367$, $df = 22$, $P > 0.05$, $n = 12$) (Figure 4.6).

The interdune areas had higher relative density of high grazing value species, with *D. seriata* being twice as much and *B. nigropedata* being absent from the dune areas (Table 4.4).

Table 4.4: Relative density (%) of perennial grass species with grazing value in relation to frost occurrence

Treatment	Grazing value	Dune	Interdune
<i>B. nigropedata</i>	High	0	2.1
<i>D. seriata</i>	High	18.1	41
<i>A. meridionalis</i>	Average	2.1	7.6
<i>E. lehmanniana</i>	Average	0.7	1.4
<i>M. repens</i>	Average	3.5	5.6
<i>P. kalaharensis</i>	Average	1.4	2.1
Treatment	Grazing value	Dune	Interdune
<i>T. schinzii</i>	Average	2.8	5.6
<i>Stipagrostis</i> sp	Average/ low	34	17.3
<i>A. stipitata</i>	Low	17.4	2.1
<i>E. jeffreysii</i>	Low	1.4	1.4
<i>E. pallens</i>	Low	16.7	12.5

Note: Field identification of *Stipagrostis* spp was difficult, therefore they were lumped

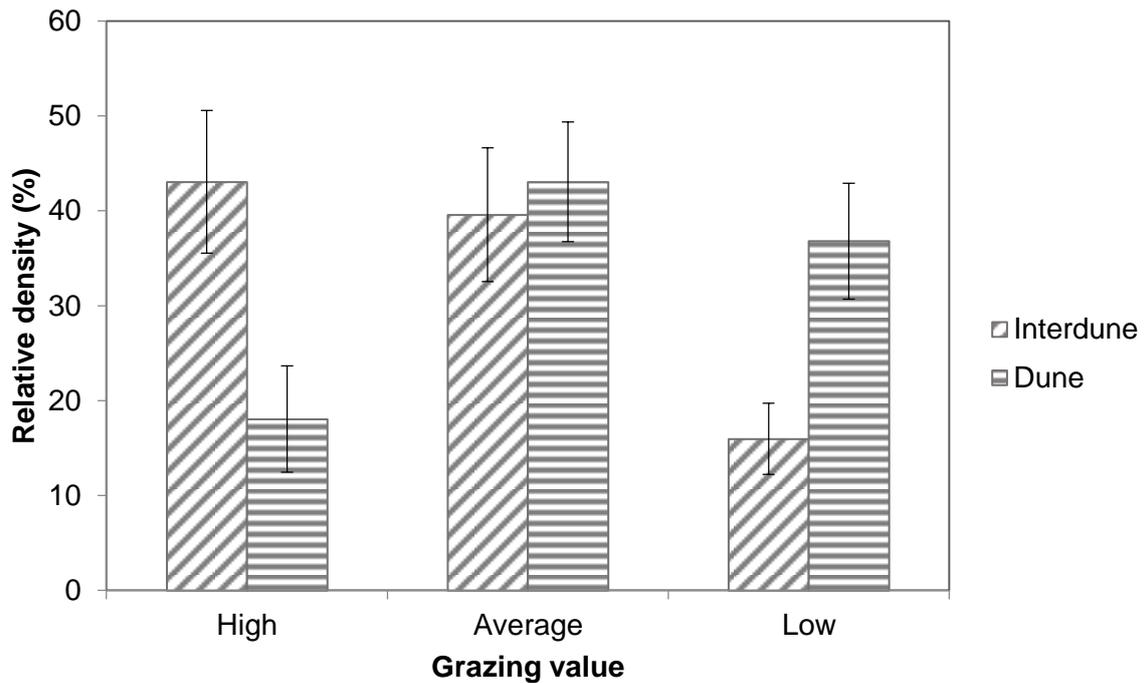


Figure 4.6: Relative density in different grazing value categories in relation to frost occurrence

(f) Woody cover

Total woody cover was significantly ($T = -3.334$, $df = 22$, $P < 0.05$, $n = 12$) higher on the dune areas (54.2 %) than the interdune areas (40.8 %) (Figure 4.7). Mean woody cover contributed by the different height classes differed significantly ($P < 0.05$) in all the height classes except in the 2–3 m height class. Woody cover in the < 2 m class was significantly greater in the interdune areas and in the > 3 m class woody cover was greater in the dune areas (Figure 4.8). *T. sericea* had almost double as much relative cover in the interdune areas, with other species such as *O. pulchra* and *A. ataxacantha* having higher relative cover on the dune areas (Table 4.5).

Table 4.5: Relative woody cover (%) of woody species in relation to frost occurrence

Woody species	Dune	Interdune
<i>A. ataxacantha</i>	16.3	0.4
<i>Acacia erioloba</i>	0	0.7
<i>A. fleckii</i>	0.2	0
<i>B. petersiana</i>	1.5	0
<i>B. africana</i>	11.8	11.7
<i>C. apiculatum</i>	0.5	0.7
<i>C. collinum</i>	5.5	9.1
<i>C. psidioides</i>	8.3	5.4
<i>G. avellana</i>	0.2	0
<i>G. flavescens</i>	2.6	0.3
<i>G. retinervis</i>	4.8	3.1
<i>O. pulchra</i>	7.6	2
<i>O. paniculosa</i>	0	1
<i>P. africanum</i>	1.1	0
<i>P. nelsii</i>	5.8	0.7
<i>S. tenuinervis</i>	0.5	0
<i>T. sericea</i>	32.9	64.5
<i>Ximenia caffra</i>	0.2	0
<i>Z. mucronata</i>	0.2	0.3

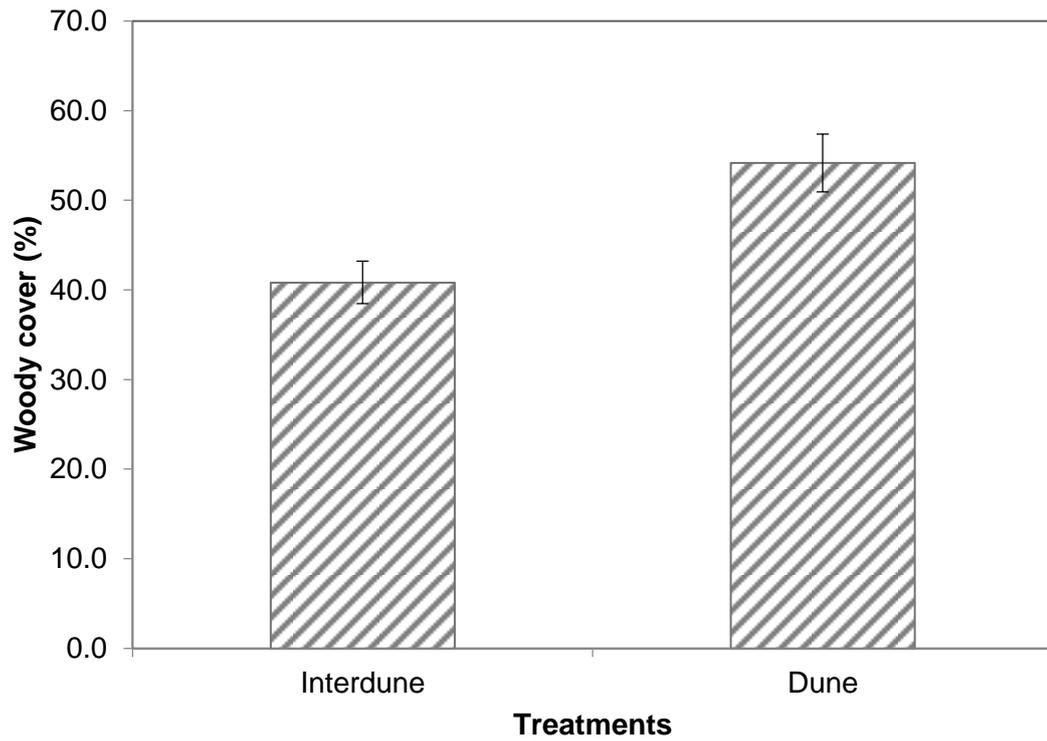


Figure 4.7: Total woody cover (%) in relation to frost occurrence

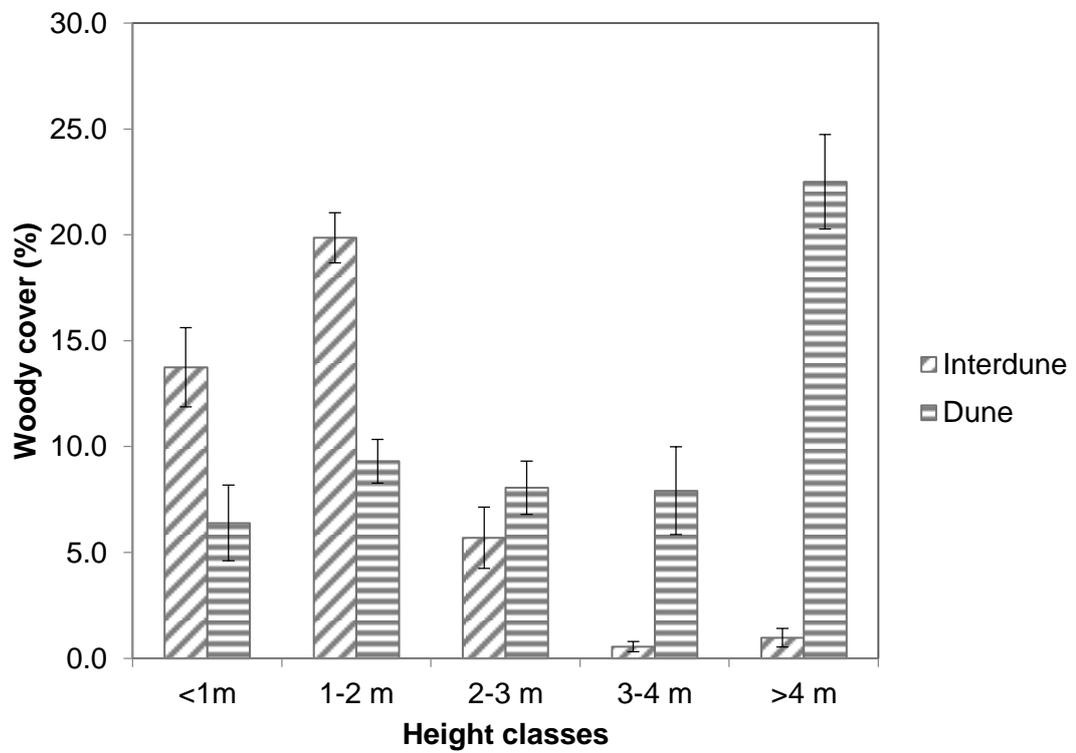


Figure 4.8: Woody cover (%) contributed by the different height classes in relation to frost occurrence

(g) Species composition

i. Perennial grass species

The HCA separated the perennial grass species into 3 main clusters at about 38% similarity, somewhat grouping the interdune areas from the dune areas (Figure 4.9).

Cluster 1 consists mainly of interdune areas and is characterised by transects with relatively low densities of the good forage species *D. seriata* and high densities of undesirable forage species such as *E. pallens* and *P. kalaharensis*.

Cluster 2 is also mainly made of interdune areas but with a high relative density of *D. seriata*.

Cluster 3 consists predominantly of dune areas with transects that have higher relative densities of undesirable grass species such as *A. meridionalis*, *A. stipitata* and *E. pallens*.

The NMS ordination revealed that frost occurrence, calcium, organic carbon, magnesium and clay are the main environmental variables responsible for driving differences in relative density of different grass species between the interdune and dune areas (Figure 4.10).

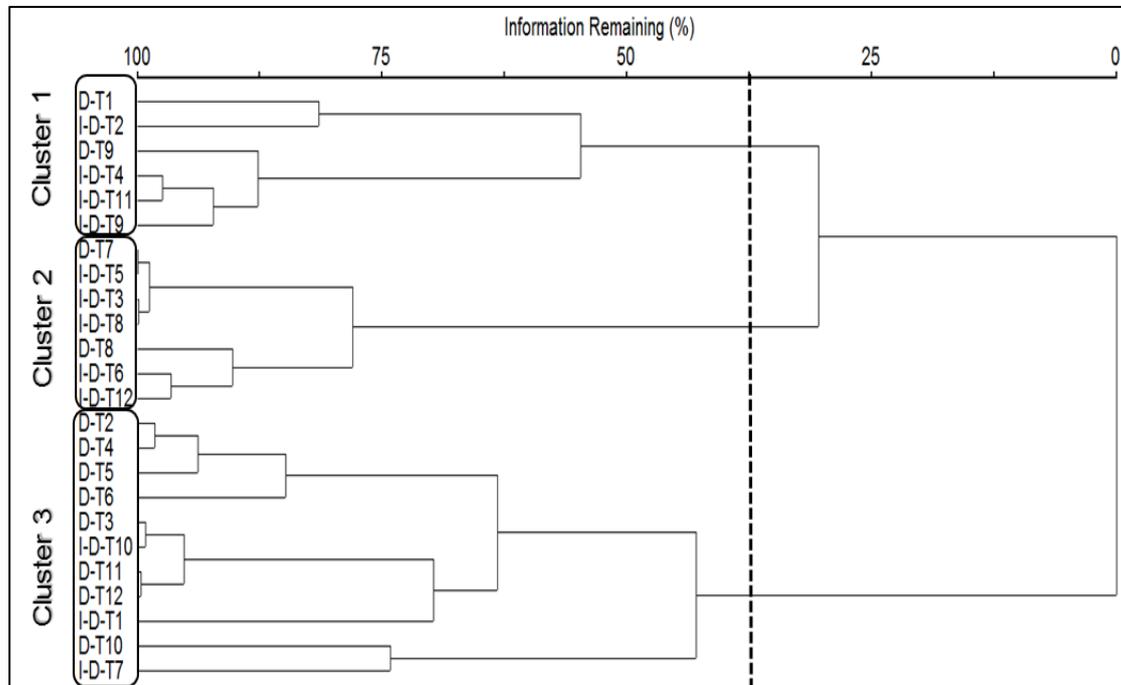


Figure 4.9: HCA dendrogram showing a classification of perennial grass species into 3 main clusters at about 38% similarity (62% information remaining). D= dune areas, ID= Interdune areas, while the letter & number represent the transect numbers, i.e. T1= transect 1.

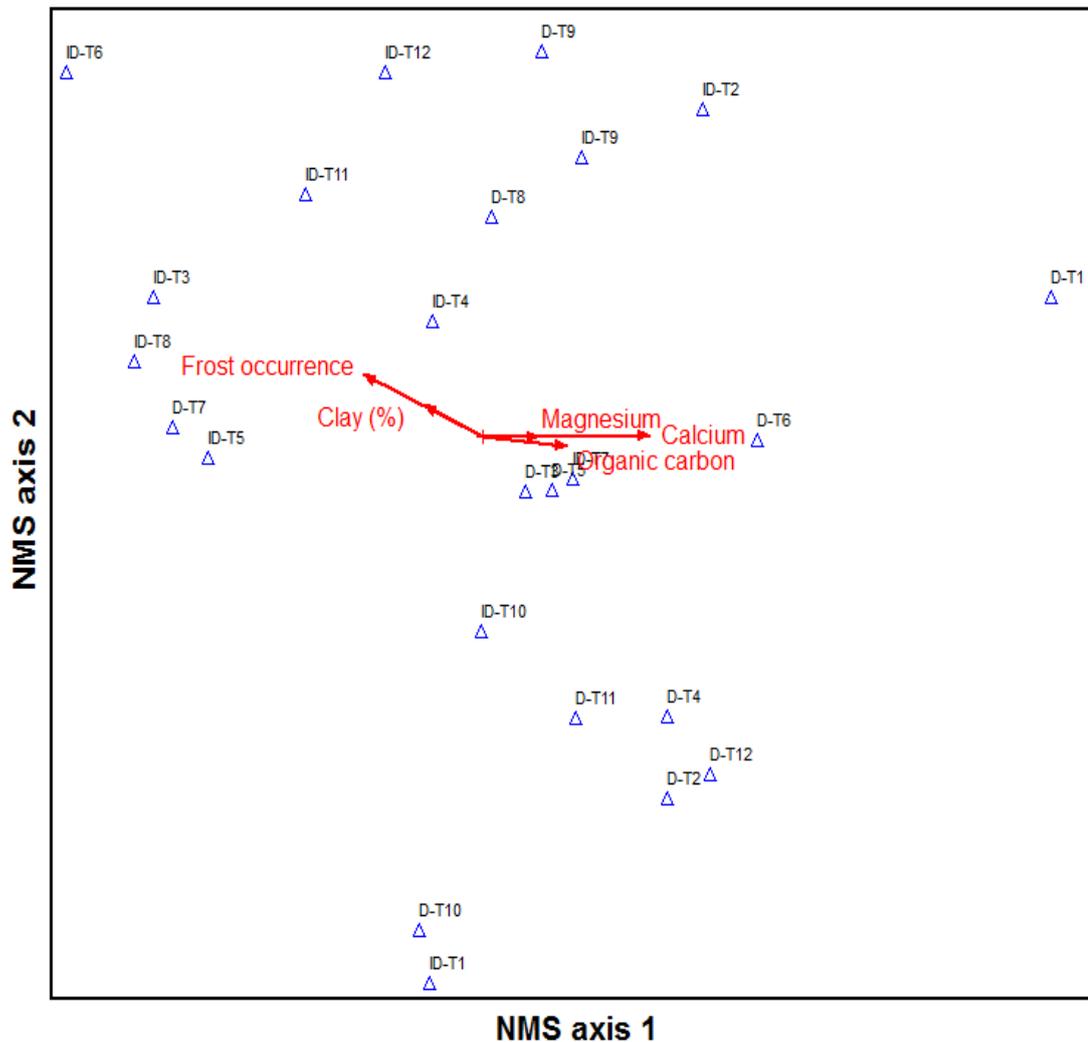


Figure 4.10: NMS joint plot for perennial grass species composition in relation to various environmental variables at r^2 cut off= 0.1. D= dune areas, ID= Interdune areas, while the letter & number represent the transect numbers, i.e. T1= transect 1.

ii. Woody plants

The HCA separated the woody species into 2 main clusters at about 13% similarity, representing mainly the interdune areas and the dune areas (Figure 4.11).

Cluster 1 consists only of the dune areas that have transects with high woody cover of *A. ataxacantha*, *O. pulchra*, *P. africanum* and *P. nelsii*. It also has transects with low cover of the following woody species: *T. sericea* and *C. collinum*.

Cluster 2 is made up of all the interdune areas and with a few dune areas. These transects have quite low woody cover of *A. ataxacantha*, *O. pulchra* and *P. nelsii* but higher woody cover of *T. sericea*, *C. collinum* and *B. africana*.

Frost occurrence was the only environmental variable responsible for driving differences in relative woody cover between the interdune and dune areas as

revealed by the NMS ordination. There is also a clear separation of the two treatments such that the dune areas are mainly to the left of the frost occurrence vector and the interdune areas are to the right of it (Figure 4.12).

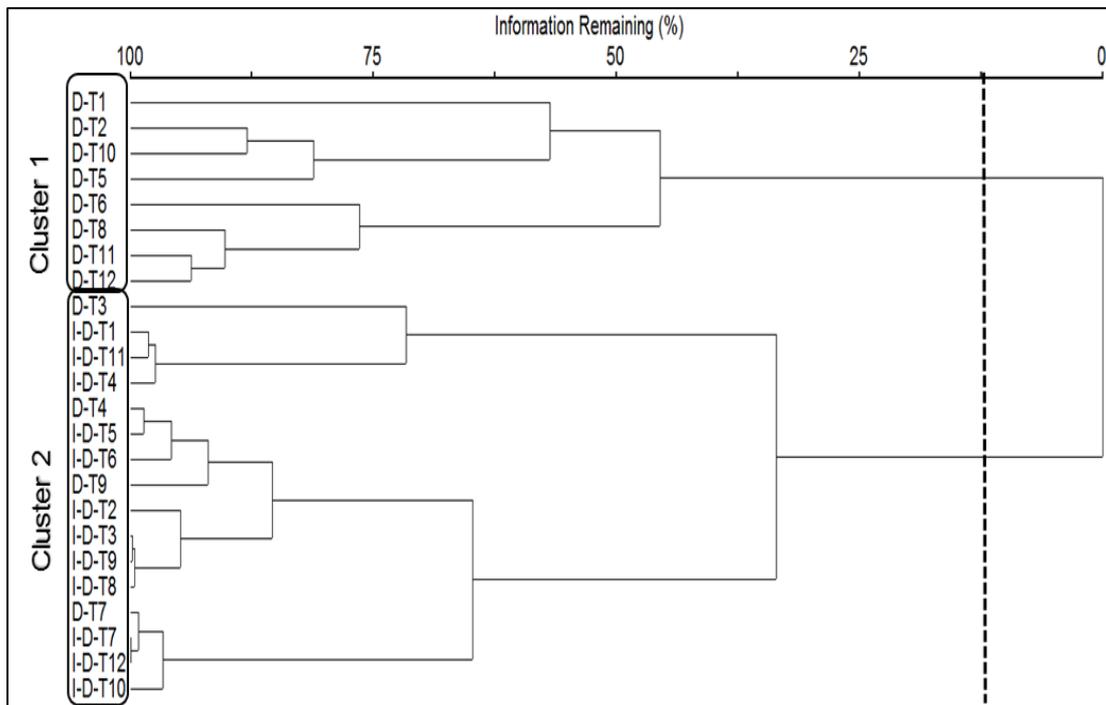


Figure 4.11: HCA dendrogram showing a classification of woody species into 2 clusters at about 13% similarity (87% information remaining). D= dune areas, ID= Interdune areas, while the letter & number represent the transect numbers, i.e. T1= transect 1.

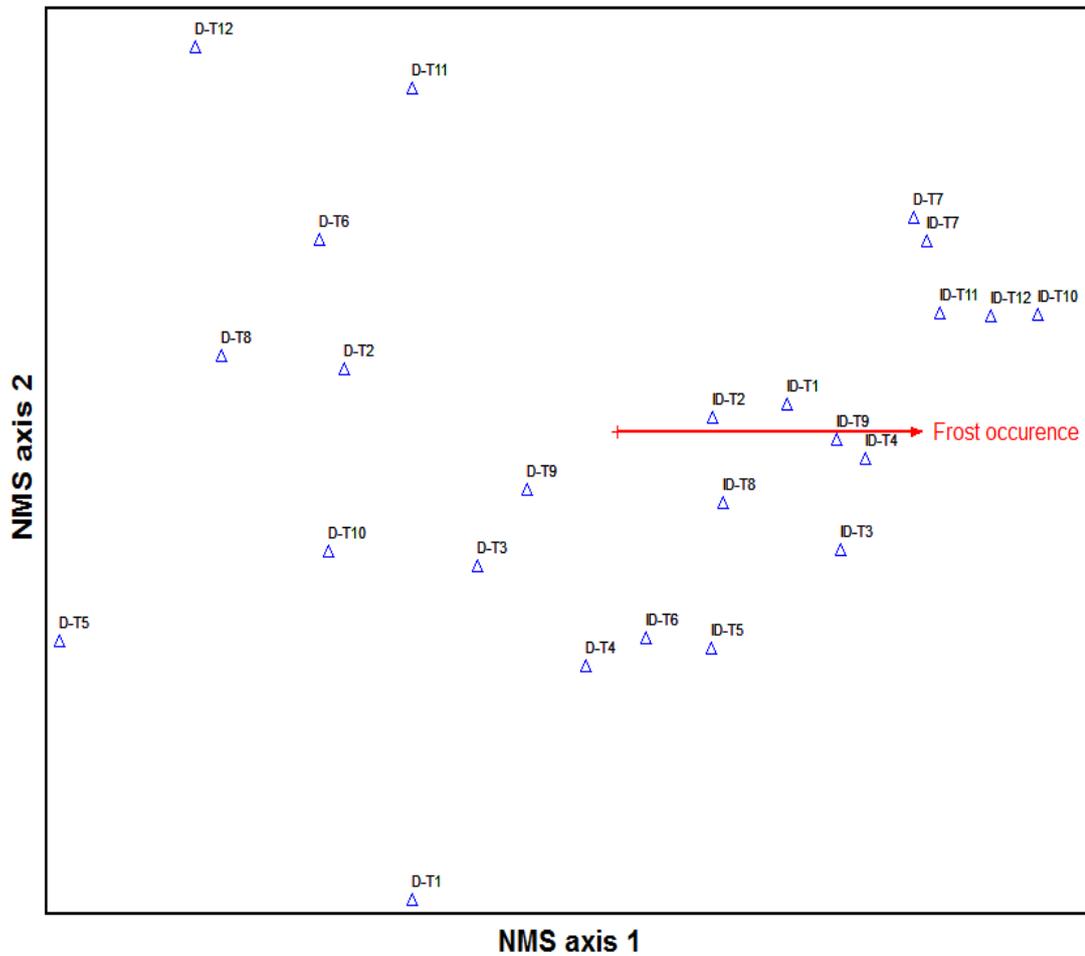


Figure 4.12: NMS joint plot for woody species composition in relation to various environmental variables at r^2 cut off= 0.2. D= dune areas, ID= Interdune areas, while the letter & number represent the transect numbers, i.e. T1= transect 1.

4.6 Discussion

4.6.1 Effects of frost on perennial grasses in a semi-arid savanna woodland

Most studies usually only take into account the effects of low temperatures (freeze and frost events) on the woody component and exclude other life forms such as grasses (Bannister, 2010). The perennial grass density was about twice as much in the interdune areas compared to the dune areas (Figure 4.2). This could be because grasses are normally dormant during winter when frost occurs and are thus not damaged (Trollope, 2003; Snyder & de Melo-Abreu, 2005). Soil nutrients could be one factor that is responsible for the observed differences. As the interdune areas are low-lying and the dune areas occur on higher elevations there is a possible soil catena influence (Scholes & Walker, 1993; Brands, Hoest & Marsh, 2000; AL-Ismaily & AL-Maktoumi, 2011). The slow accumulation of water and nutrients flowing into the interdune areas from the dune areas may result in an increase in perennial grass density (Brands et al., 2000). However, from the soil analysis results (Table 4.3) there were no significant differences in all the soil properties, ruling out soil properties as being responsible for the differences in perennial grass density. Although moisture retention and addition could result in new grass shoots, which could account for higher grass density in the interdune areas.

The lower canopy cover, and resultant reduced competition for light between woody plants and the perennial grasses may explain this (Belsky, 1994; van der Waal et al., 2009). The top-kill of woody plants by frost significantly reduces woody cover (Figure 4.7) and allows more light penetration to the herbaceous layer (Scholes & Walker, 1993; Nepolo & Mapaure, 2012). This may enhance germination, establishment and growth of new grass species (Nepolo & Mapaure, 2012) such as *B. nigropedata* that was not encountered in dune areas possibly due to the higher woody cover that may intercept most of the light. This probably contributed to the higher relative density of such palatable grass species such as *D. seriata* in the interdune areas (Figure 4.6; Table 4.4).

Both areas had quite a low grass biomass (Figure 4.5) which could be a result of intense competition for resources with the high density of woody plants (Riginos, 2009; Zimmerman et al., 2010). The dominant woody species in the study area is *T. sericea* which has a shallow root system (Lutibezi, 2016). It may be the main competitor for soil water and nutrients with perennial grasses and other shallow rooted plants (Hipondoka & Versfeld, 2006).

The absence of fire for 24 years could also explain the low grass biomass in the interdune and dune areas. Chapter 3 emphasized the positive impact of fire on grasses, through burning of moribund grasses thus reducing shade and competition between established

plants (Mapiye et al., 2008; Zimmermann et al., 2010; Gul et al., 2014). This stimulates regrowth of new shoots, temporarily increases above-ground productivity and increases biomass production (Scholes & Walker, 1993; Zimmermann et al., 2010; Gul et al., 2014). Without defoliation by fire and grazing, plant senescence and accumulation of moribund grass may increase tuft mortality through self-shading which reduces irradiance and consequently suppresses initiation and survival of tillers adversely affecting biomass production (Zimmermann et al., 2010). Therefore, although there are good grazing value species, because they have accumulated moribund material they may be unappealing to animals and are thus rarely utilized (Tomor & Owen-Smith, 2002). Zimmermann et al. (2010) found low herbivore densities at a site burned 7 years ago in Etosha National Park, which shows a low probability of grazing in areas that have not been burned in a long time.

The HCA separated the perennial grasses into three main clusters with a relatively good separation of the interdune areas from the dune areas (Figure 4.9). The interdune areas separated into two clusters with one having a higher density of good forage grass species, while the other had higher densities of low grazing value grass species. The NMS ordination also revealed that frost occurrence was one of the main factors responsible for differences in relative grass density of the grass species (Figure 4.10). As discussed earlier, frost indirectly contributes to higher density of grasses through reduced competition for light with the woody plants (Belsky, 1994; van der Waal et al., 2009). Although there were no statistical differences in soil properties between the interdune and dune areas, the ordination results showed that calcium, organic carbon, magnesium and clay also contributed to differences in relative density of the grass species. This is likely due to the soil catena which may have played a role in transporting these soil nutrients (Yeaton et al., 1986 in Scholes & Walker, 1993). Grass species distribution may change along a catena due to slight differences in soil properties as well as moisture (Yeaton et al., 1986 in Scholes & Walker, 1993).

4.6.2 Effects of frost on woody plants in a semi-arid savanna woodland

The interdune areas had significantly colder temperatures below zero degrees Celsius, although surprisingly the dune areas experienced very cold temperatures as well (Table 4.2). The extremely cold temperatures in the interdune areas were due to topography as colder air settles in the low-lying areas reducing the temperatures (de Long, 2001; Mendelsohn & el Obeid, 2005; Henschel et al., 2016; Reddick, undated). The number of days that experienced temperatures below freezing was 89 in the interdune areas and 80 in the dune areas (Table 4.2), which highly contrasts 6-10 days according to Mendelsohn & el Obeid (2005). This could be due to a much colder winter experienced in 2015 in the study site with the coldest

temperature being -14.6°C recorded in the interdune areas and -9.1°C recorded at the WPP SASSCAL weather station the same night 0(www.sasscalweathernet.org).

Frost, like fire in the study area affects woody plants mainly through killing of above-ground plant tissues forcing some plants to resprout from the base (Smit, 1990; Holdo, 2007; Wakeling et al., 2012). Total woody density was not significantly different (Figure 4.3) between the interdune and dune areas. It is rare for whole-tree mortality to occur after exposure to frost (Whitecross et al., 2012) with only the above-ground biomass being lost (Wakeling et al., 2012). This suggests that woody plants in this savanna woodland are adapted to frost occurrence. Therefore, woody plants survive but remain in shorter height classes increasing the time required to escape effects of further frost and fire (Wakeling et al., 2012). This could be the reason for such a high number (about 23000 individuals/ ha) of $< 1\text{ m}$ woody plants in the interdune areas (Figure 4.4a).

Where frost occurs less frequently woody plants are able to grow to heights $> 4\text{ m}$, resulting in the dune areas having significantly higher woody density of this height class (Figure 4.4b). Vegetation established in low-lying areas is at greater risk of frost damage especially that at $< 2\text{ m}$ tall (Whitecross et al., 2012; Henschel et al., 2016). Hence, the woody cover in the interdune area is significantly higher for height classes $< 2\text{ m}$ and significantly lower in the height classes $> 3\text{ m}$ (Figure 4.8). Like recent fires, the top-kill caused by frost therefore creates open areas and keeps woody plants confined in what can be termed a “freeze trap” (Whitecross et al., 2012). This may significantly increase the amount and height of fuel loads, which may extend ground fires into tree crowns, leading to more intense fires (Holdo, 2007). In contrast, vegetation growing slightly on higher elevation even with low temperatures has less chance of being affected (Whitecross et al., 2012; Henschel et al., 2016). Thus, woody plants are able to grow more easily into taller height classes and contribute a higher woody cover as canopies grow bigger (Whitecross et al., 2012).

The HCA grouped most of the dune areas together and grouped all the interdune areas with a few dune areas (Figure 4.11). The cluster with dune areas had higher woody cover of *A. ataxantha* and *O. pulchra* as compared to cluster 2 that had low woody cover of these but higher woody cover of *T. sericea*. This suggests that frost occurrence plays a major role in the abundance of different woody species based on how frost tolerant they are. This was also revealed by the NMS ordination that frost occurrence was the only factor responsible for differences in relative woody cover of the woody species as there was also a clear separation of the two treatments (Figure 4.12). Frequent and severe frost can have a significant influence on the distribution and abundance of savanna woody species (Whitecross et al., 2012), with frost-sensitive species being confined to higher elevations (Henschel et al.,

2016). In the interdune areas woody plants within the freeze trap are top-killed during winter when temperatures drop below 0 °C losing their overall height and canopy cover (Whitecross et al., 2012). The frost damaged woody plants persist through resprouting and the repeated frost events may result in a population of highly resilient coppiced trees, although with a low canopy cover (Holdo, 2006). *T. sericea* was found to be the dominant woody species in the interdune areas (Table 4.5), due to its high tolerance to frost as it resprouts readily when damaged (Holdo, 2006). On slightly higher elevations that may also experience cold temperatures as was observed in the study area (Table 4.1) woody plants had higher canopy cover. Frost damage is thus less severe to woody species on the dunes as they are likely beyond the freeze trap and may have bigger stems that buffer them against occasional cold temperatures (Holdo, 2005; Whitecross et al., 2012). For example, *A. ataxacantha* and *O. pulchra* were found to have higher woody cover on the dunes (Table 4.5) suggesting less tolerance levels for frost in this savanna woodland. However, *O. pulchra* is said to be highly frost resistant in other ecosystems such as the Miombo woodlands (Holdo, 2007).

4.7 Conclusion

Frost occurrence has an indirect impact on the grass component in this savanna woodland. A higher perennial grass density was observed in the interdune areas, likely due to top-kill of woody plants by frost which increases light penetration to the grass layer. In addition, desirable grasses such as *D. seriata* and *B. nigropedata* also had higher relative densities in the interdune areas as an indirect effect of frost occurrence. Besides some soil properties, grass species composition was thus mainly influenced by frost occurrence towards more palatable species. Both the interdune and dune areas had relatively low grass biomass, which could be attributed to competition between such high numbers of woody plants and the grass layer, with woody plants being usually better competitors. The absence of fire for many years could have also resulted in such low grass biomass due to the accumulation of moribund material which shades and suppresses new tiller growth.

Like fire, frost mainly top-kills woody plants forcing them to resprout from the base and confining them in a freeze trap. This way frost creates an open savanna dominated by frost-tolerant gullivers such as *T. sericea*. Woody plants occurring on slightly higher elevations are less affected by frost and grow into taller height classes with bigger canopies; this is despite these areas also experiencing occasionally very low temperatures. Unlike the current fire regime, frost occurrence seems to be a key limiting disturbance in the distribution of woody species such as *O. pulchra* and *A. ataxacantha*.

CHAPTER 5

CONCLUSIONS & RECOMMENDATIONS

5.1 Conclusions

The aim of this study was to investigate how fire history and frost occurrence affect vegetation structure and species composition in a savanna woodland at the arid end of the scale. The relatively well known fire history of the study area and the clear dune system in some parts of the study area provided an opportunity to carry out this research. The study was part of a broader project investigating the effects of fire history on ecosystem processes and biodiversity. The findings from this study contribute to our understanding of how fire and frost affect vegetation in such woodland ecosystems. Based on this study frost may be as important as fire as a disturbance affecting vegetation structure and species composition. These findings will provide insights on how frost affects perennial grasses and woody plants and be a building block towards understanding savanna woodlands in this aspect.

Based on this SFT substitution study fire increases grass density, improves forage quality but temporarily reduces grass biomass which rapidly recovers. The post-fire regrowth attracts animals to recently burned areas, which allows other recently burned sites to recover full grass biomass after one growing season. Fire can therefore be used to temporarily redistribute herbivores into recently burned areas, which may improve animal condition and possibly increase carrying capacity. The current fire history does not change overall grass species composition, but slightly shifts grasses towards more palatable species such as *D. seriata*. In the absence of fire perennial grass density, grass biomass and quality decrease, largely as a result of moribundity (which causes self-shading), self-thinning and increased competitive pressure which may result in tuft mortality.

Savanna woody vegetation is well adapted to fire and persists as gullivers, which is the case in the study area. Fire in this savanna woodland did not significantly reduce woody density or change the species composition, but acted mainly on the structure. Fire through top-kill reduces the height of woody plants within the flame zone to browsable heights and resprouts are highly nutritious. Thus, although fire did not result in a significant reduction of woody plant density and cause a change in species composition in this system, it had important effects on structure, effectively maintaining an open savanna through top-kill.

Figure 5.1 below is a synthesis of the main findings; it shows how fire causes a structural change of the vegetation in this semi-arid savanna woodland. With time since last burn the grass density decreases, while grass biomass is significantly reduced temporarily by fires. The post-fire regrowth attracts herbivores as it is highly palatable and nutritious. This allows

for other recently burned areas such treatment 2 to rest and rapidly recover lost grass biomass and without fires over the years grass biomass and presumably productivity then decreases. Although total woody density was not significantly reduced, overall woody cover increased with time since last burn. Recent fires top-kill woody plants but without fires over the years individual woody plant canopies increase resulting in a more closed savanna woodland.

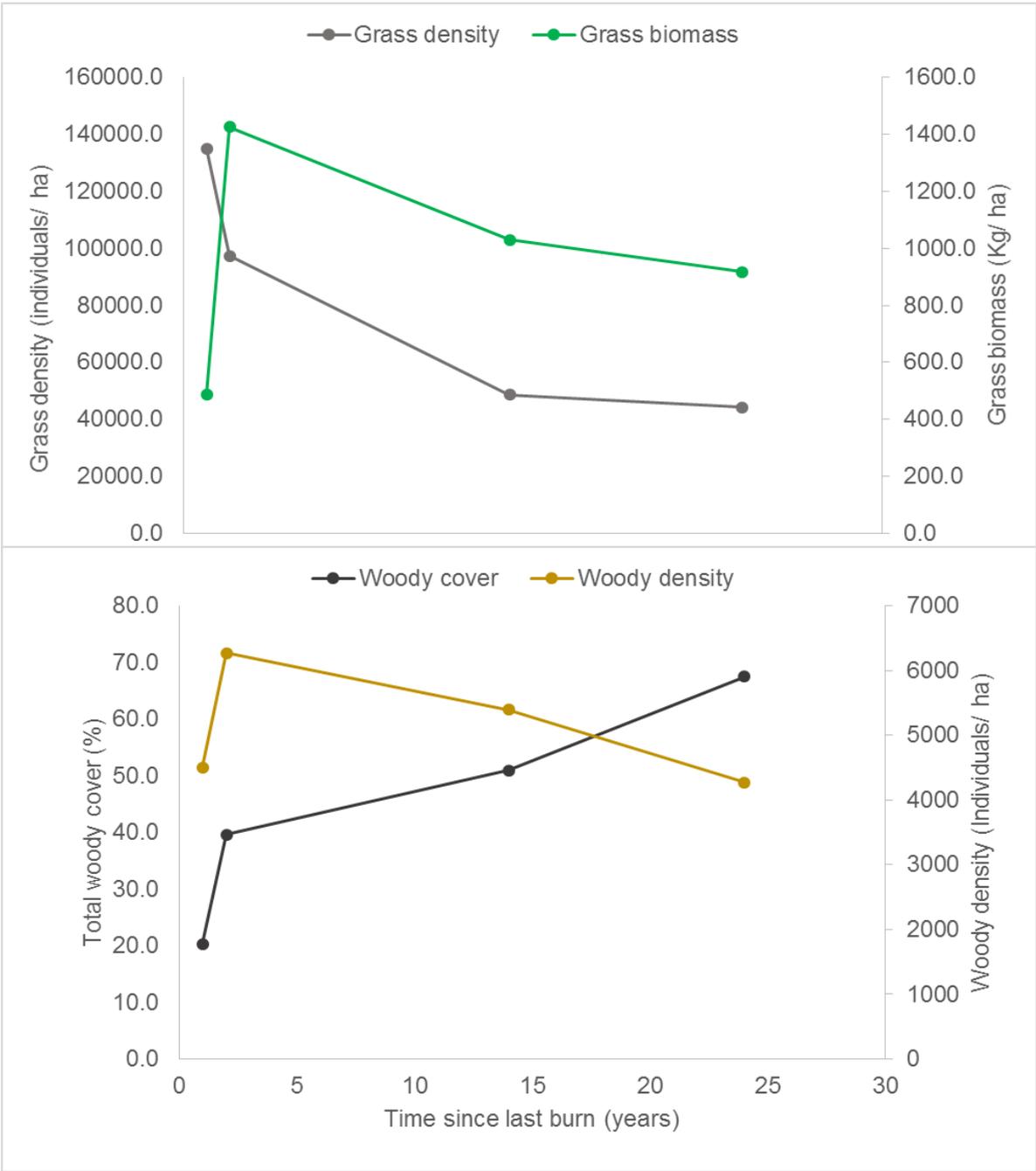


Figure 5.1: Grass density, grass biomass, woody density and woody cover in relation to time since last burn (years)

Frost occurrence on the other hand, seems to indirectly positively influence grass density and grass species composition in the interdune areas through increased light penetration. An increase in perennial grass density was observed in the interdune areas, presumably due to top-kill of woody plants by frost which allows more light penetration to the grass layer. In addition, palatable grasses such as *D. seriata* and *B. nigropedata* were more abundant in the interdune areas. Therefore, grass species composition was mainly influenced indirectly by frost occurrence, with calcium and soil organic carbon having a relatively minor effect. Both the interdune and dune areas had lower grass biomass in comparison to all the fire treatments. This could be attributed to competition between the high density of woody plants and the grass layer. The absence of fire for many years in this dune-interdune system may be the reason for such low grass biomass, highlighting the importance of fire.

Like fire, frost mainly top-kills woody plants forcing them to resprout from the base and confining them in a freeze trap, which explains the high numbers of < 1 m tall woody plants in the interdune areas where frost occurrence is more prevalent and severe. This way frost creates open areas dominated by high densities of resprouting frost-tolerant woody plants. In contrast, woody plants on the dune areas experience less severe frost, allowing individuals to escape the freeze trap into taller height classes and grow bigger canopies. Surprisingly, the dune areas also experienced very low temperatures during the study period. While frost occurrence in this savanna system has similar effects on the structure of the woody component as fire, it also significantly alters the species composition as the HCA and ordination results revealed. Frost-tolerant woody species such as *T. sericea* dominated in the interdune areas, while other species such as *O. pulchra* and *A. ataxacantha* were almost absent in the interdune areas but more on the dune areas, suggesting that they are more frost-sensitive.

5.2 Recommendations

5.2.1 Fire management for the WPP

Results suggest that an increase in prescribed burning in some of the areas in the WPP will improve the quality and production of forage and available browse for herbivores and also maintain an open savanna through reduced height and canopy cover. Through regular burning unpalatable grasses are suppressed, moribund grass removed and the range improved temporarily.

The current fire regime does not change species composition, but there is a slight shift towards more palatable grasses in recently burned areas, rapid recovery of grass biomass which increased herbivore utilization. Therefore, burning improves the range condition by temporarily increasing the crude protein content, palatability and increasing the abundance of valuable forage species while decreasing undesirable species. Herbivores are attracted to this post-fire regrowth and readily graze it. This has important implications for the park as park management can use fire to attract animals to underutilized areas, reducing the grazing pressure off highly utilized areas. This will allow previously burned areas to rest and recover lost grass biomass. The improved range condition will result in increased animal production and condition and generally increase the carrying capacity as well as a more efficient transfer of energy along trophic levels.

The areas burned 14 and 24 years (including the dune and interdune areas) would benefit from burning to improve the range condition in these areas and increase utilization, however, due to a low grass biomass (fuel load) that is sparsely distributed it is likely that the fire will be of low intensity and patchy. However, if it is achievable (after good periods of rainfall) these areas would benefit from more frequent fires such as those of treatment 1, but habitat diversity should be taken into consideration as different animals require different habitat types (shady areas vs more open areas). An alternative to burning would be to consider a recommendation given by Mukaru (2009) to use salt licks by placing them in such underutilized areas as a way to encourage animals to utilize them more often and reduce degradation around waterholes, while maintaining grass vigour.

Recent fires did not significantly reduce overall woody density, but rather acted on the structure by reducing the height and canopy cover. These findings show that the current fire history will not reduce overall woody density, probably also due to generally low fuel loads. It only maintains the WPP savanna woodland in an open state by reducing canopy cover and height of woody plants. However, park management could wait for a high rainfall year which

is likely to result in an increase in grass biomass sufficient enough to result in a significant decrease of woody density.

5.2.2 Further research

- (a) Fire intensity is rarely measured in African savannas, despite its importance for understanding how fire affects vegetation structure and composition. The lack of fire intensity measurements in the study area limited the possible explanations for the results found especially on the woody component. It is therefore recommended that a study or experiment be carried out to determine how intense fires are in this semi-arid savanna woodland.
- (b) This study measured standing biomass which was affected mainly by grazing, especially in the recently burned areas. A study looking at actual grass productivity after defoliation by fire and/ or grazing is recommended to determine the time it takes for grasses to recover full biomass, which could be done using exclosures.
- (c) Further research should be done to better understand how frost affects woody species. The study should look at which species are severely affected and how much top-kill occurred during winters of different severity.
- (d) Park management is also encouraged to keep well-documented records of fire occurrence, extent, intensity etc. This information is important for future studies and for long-term records. Such information is also important in trying to understand more accurately how fire is altering vegetation dynamics in this semi-arid savanna woodland.
- (e) Future research projects on ecosystem processes and biodiversity are encouraged to consider using the same line transects as they are marked physically and GPS coordinates are available (Appendix 1). This can contribute on further understanding this savanna woodland in a more holistic approach. Long-term vegetation monitoring should also be done on the same transects to see how it changes over the years.

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APPENDICES

Appendix 1. GPS coordinates for the beginning and end of transects surveyed

Treatment	Transect	Beginning	End
1	1	S 20.34940 E 17.36468	S 20.34931 E 17.36276
1	2	S 20.34717 E 17.36301	S 20.34722 E 17.36112
1	3	S 20.33695 E 17.35962	S 20.33693 E 17.35771
1	4	S 20.32828 E 17.35189	S 20.32824 E 17.35382
1	5	S 20.32043 E 17.39806	S 20.31859 E 17.39804
1	6	S 20.34509 E 17.40938	S 20.34506 E 17.41131
2	1	S 20.29462 E 17.40840	S 20.29278 E 17.40841
2	2	S 20.29152 E 17.39159	S 20.28969 E 17.39159
2	3	S 20.29130 E 17.38774	S 20.28947 E 17.38774
2	4	S 20.28523 E 17.353268	S 20.28522 E 17.35077
2	5	S 20.31055 E 17.35288	S 20.31052 E 17.35098
2	6	S 20.30417 E 17.35312	S 20.30415 E 17.35119
14	1	S 20.31953 E 17.34557	S 20.31952 E 17.34748
14	2	S 20.32588 E 17.3394	S 20.32764 E 17.33596
14	3	S 20.32657 E 17.32745	S 20.32834 E 17.32745
14	4	S 20.32821 E 17.31689	S 20.32999 E 17.31689
14	5	S 20.32523 E 17.31526	S 20.32520 E 17.31332
14	6	S 20.33197 E 17.33899	S 20.32928 E 17.31330
24	1	S 20.34939 E 17.35604	S 20.34938 E 17.35758
24	2	S 20.35646 E 17.35784	S 20.35646 E 17.35974
24	3	S 20.33073 E 17.34793	S 20.33069 E 17.34984
24	4	S 20.33423 E 17.31628	S 20.33241 E 17.31626
24	5	S 20.32704 E 17.34859	S 20.32843 E 17.34854
24	6	S 20.32930 E 17.31523	S 20.3312 E 17.33904
Interdune	1	S 20.39421 E 17.32702	S 20.39433 E 17.32795
Interdune	2	S 20.39304 E 17.31312	S 20.39214 E 17.31306
Interdune	3	S 20.39340 E 17.31447	S 20.39251 E 17.31459
Interdune	4	S 20.39272 E 17.27712	S 20.39183 E 17.27698
Interdune	5	S 20.39398 E 17.32435	S 20.39308 E 17.32420
Interdune	6	S 20.39422 E 17.32191	S 20.39332 E 17.32186
Interdune	7	S 20.41166 E 17.26954	S 20.41156 E 17.26861

Treatment	Transect	Beginning	End
Interdune	8	S 20.39414 E 17.27392	S 20.39400 E 17.27298
Interdune	9	S 20.41944 E 17.29861	S 20.42032 E 17.29867
Interdune	10	S 20.42076 E 17.29656	S 20.42160 E 17.29690
Interdune	11	S 20.42238 E 17.29391	S 20.42326 E 17.29381
Interdune	12	S 20.39343 E 17.31822	S 20.39254 E 17.31807
Dune	1	S 20.41520 E 17.31420	S 20.41603 E 17.31456
Dune	2	S 20.39193 E 17.27312	S 20.39105 E 17.27315
Dune	3	S 20.39832 E 17.32747	S 20.39824 E 17.32839
Dune	4	S 20.40068 E 17.32740	S 20.40060 E 17.32835
Dune	5	S 20.40716 E 17.33006	S 20.40724 E 17.33101
Dune	6	S 20.41360 E 17.31872	S 20.41443 E 17.31899
Dune	7	S 20.42441 E 17.27427	S 20.42531 E 17.27444
Dune	8	S 20.39268 E 17.29144	S 20.39180 E 17.29161
Dune	9	S 20.40665 E 17.27130	S 20.40678 E 17.27038
Dune	10	S 20.39838 E 17.27383	S 20.39853 E 17.27288
Dune	11	S 20.39559 E 17.27408	S 20.39553 E 17.27312
Dune	12	S 20.41307 E 17.32067	S 20.41393 E 17.32087

Appendix 2. Rainfall and temperature readings recorded at the WPP SASSCAL weather station

Table 1. Total rainfall recorded for 2012-2015 (www.sasscalweathernet.org)

Year	Total rainfall (mm)
2012-2013	280
2013-2014	913.9
2014-2015	212.7

Table 2. Average temperature readings and coldest temperatures recorded from 2012-2015 (www.sasscalweathernet.org)

Year	Average temp (°C)	Average min temp (°C)	Average max temp (°C)	Coldest temp (°C)
2012	19.0	3.1	31.5	-7.2
2013	19.8	2.8	32.7	-5.0
2014	18.9	3.4	30.4	-5.7
2015	20.1	2.8	32.2	-9.1

Appendix 3. List of plant species surveyed in the study area

Table 1: Woody species and where they were surveyed in the study area

No.	Woody species	Fire history treatments				Frost treatments	
		1	2	14	24	Interdune	Dune
1	<i>Acacia ataxacantha</i> DC.	Yes	Yes	Yes	Yes	Yes	Yes
2	<i>Acacia erioloba</i> E.Mey.	No	No	No	No	Yes	Yes
3	<i>Acacia fleckii</i> Schinz	Yes	Yes	Yes	Yes	No	No
4	<i>Acacia mellifera</i> (Vahl) Benth.	No	No	No	Yes	No	No
5	<i>Bauhinia petersiana</i> Bolle	Yes	Yes	Yes	Yes	Yes	Yes
6	<i>Burkea africana</i> Hook.	Yes	Yes	Yes	Yes	Yes	Yes
7	<i>Combretum apiculatum</i> Sond.	No	Yes	Yes	No	Yes	Yes
8	<i>Combretum collinum</i> Fresen.	Yes	Yes	Yes	Yes	Yes	Yes
9	<i>Combretum psidioides</i> Welw.	Yes	Yes	Yes	Yes	Yes	Yes
10	<i>Croton gratissimus</i> Burch.	No	No	No	Yes	No	Yes
11	<i>Dichrostachys cinerea</i> (L.) Wight & Arn.	No	No	No	No	No	Yes
12	<i>Diospyros lycioides</i> Desf.	No	No	No	No	Yes	No
13	<i>Grewia avellana</i> Hiern	Yes	Yes	Yes	No	Yes	Yes
14	<i>Grewia flavescens</i> Juss.	Yes	Yes	Yes	Yes	Yes	Yes
15	<i>Grewia retinervis</i> Burret	Yes	Yes	Yes	Yes	Yes	Yes
16	<i>Ochna pulchra</i> Hook.	Yes	Yes	Yes	Yes	Yes	Yes
17	<i>Ozoroa paniculosa</i> (Sond.) R.Fern & A.Fern	No	No	No	No	Yes	No
18	<i>Peltophorum africanum</i> Sond.	Yes	Yes	Yes	Yes	Yes	Yes
19	<i>Philenoptera nelsii</i> (Schinz) Schrite	Yes	Yes	Yes	Yes	Yes	Yes
20	<i>Searsia marlothii</i> (Engl.) Moffett	No	No	Yes	Yes	No	No
21	<i>Searsia tenuinervis</i> (Engl.) Moffett	Yes	No	Yes	No	No	Yes
22	<i>Terminalia sericea</i> Burch.	Yes	Yes	Yes	Yes	Yes	Yes
23	<i>Ximenia americana</i> L.	No	Yes	No	No	No	Yes
24	<i>Ximenia caffra</i> Sond.	No	No	Yes	No	No	Yes
25	<i>Ziziphus mucronata</i> Willd.	Yes	No	Yes	No	Yes	Yes

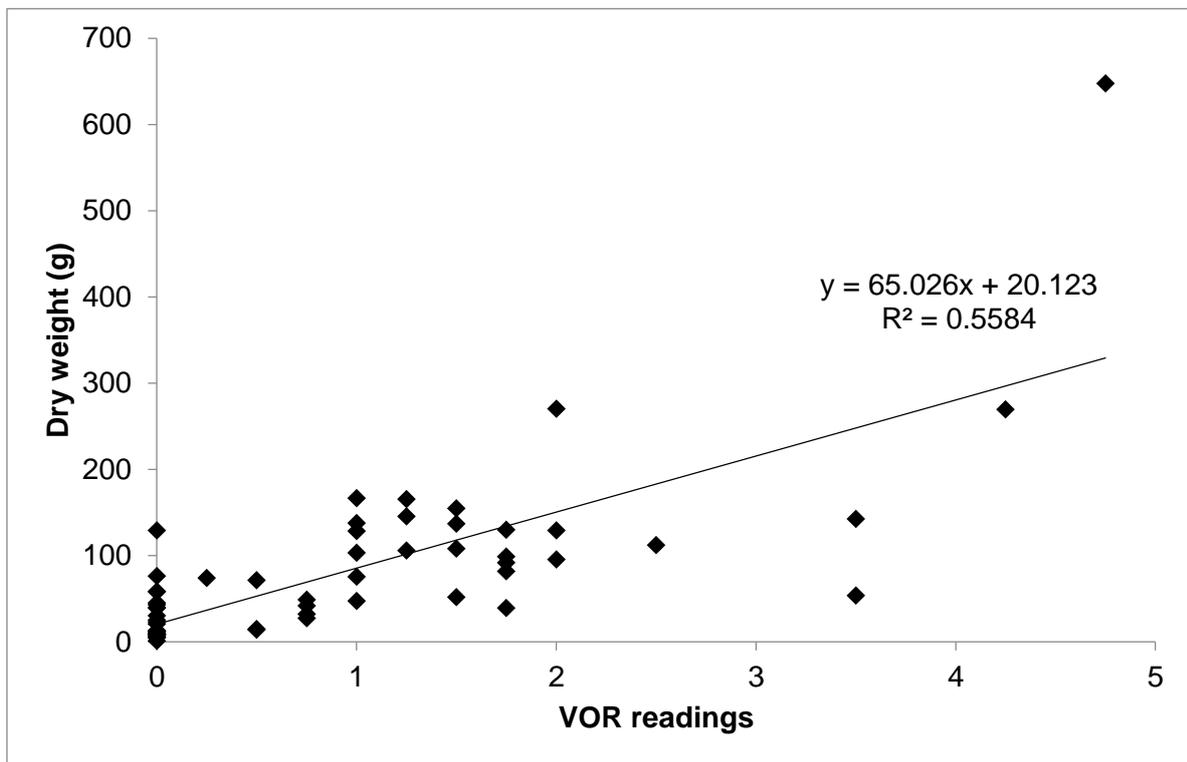
Note: The names and author citations are extracted from Klaassen & Kwembeya (2013)

Table 2: Perennial grass species and where they were surveyed in the study area

No.	Perennial grass species	Fire history treatments				Frost treatments	
		1	2	14	24	Interdune	Dune
1	<i>Aristida meridionalis</i> Henrard	Yes	Yes	No	Yes	Yes	Yes
2	<i>Aristida stipitata</i> Hack.	Yes	Yes	Yes	Yes	Yes	Yes
3	<i>Brachiaria nigropedata</i> (Ficalho & Hiern) Stapf	No	Yes	No	No	Yes	No
4	<i>Digitaria seriata</i> Stapf	Yes	Yes	Yes	Yes	Yes	Yes
5	<i>Eragrostis jeffreysii</i> , auct., sensu B.K.Simon	Yes	Yes	Yes	Yes	Yes	Yes
6	<i>Eragrostis lehmanniana</i> Nees	Yes	No	Yes	No	Yes	Yes
7	<i>Eragrostis pallens</i> Hack.	Yes	Yes	Yes	Yes	Yes	Yes
8	<i>Melinis repens</i> (Willd.) Zizka	Yes	No	Yes	Yes	Yes	Yes
9	<i>Panicum kalahareense</i> Mez	Yes	Yes	Yes	Yes	Yes	Yes
10	<i>Panicum maximum</i> Jacq.	Yes	No	No	No	No	No
11	<i>Stipagrostis hirtigluma</i> (Steud. Ex Trin. & Rupr.) De Winter	No	Yes	Yes	Yes	No	Yes
12	<i>Stipagrostis uniplumis</i> (Licht.) De Winter	Yes	Yes	Yes	Yes	Yes	Yes
13	<i>Triraphis schinzii</i> Hack.	Yes	No	Yes	Yes	Yes	Yes

Note: The names and author citations are extracted from Klaassen & Kwembeya (2013)

Appendix 4. Regression of VOR and dry weight of perennial grasses



Appendix 5. Grazing value of perennial grass species using a published index (Muller, 2007)

Species	Grazing value
<i>Brachiaria nigropedata</i>	High
<i>Digitaria seriata</i>	High
<i>Panicum maximum</i>	High
<i>Aristida meriodonalis</i>	Average
<i>Melinis repens</i>	Average
<i>Panicum kalahareense</i>	Average
<i>Eragrostis lehmaniana</i>	Average
<i>Stipagrostis uniplumis</i>	Average
<i>Triraphis schinzii</i>	Average
<i>Aristida stipitata</i>	Low
<i>Eragrostis jeffreysii</i>	Low
<i>Eragrostis pallens</i>	Low
<i>Stipagrostis hirtigluma</i>	Low