BUSH ENCROACHMENT EFFECTS ON ABOVE-GROUND BIOMASS, SPECIES COMPOSITION, PLANT DIVERSITY AND SELECTED SOIL PROPERTIES IN A SEMI-ARID SAVANNA GRASSLAND

BY

REGINA ETLA MOGASHOA

A MINI-DISSERTATION SUBMITTED IN (PARTIAL) FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE IN AGRICULTURE (PASTURE SCIENCE)

FACULTY OF SCIENCE AND AGRICULTURE
(SCHOOL OF AGRICULTURAL AND ENVIRONMENTAL SCIENCES)

AT THE
UNIVERSITY OF LIMPOPO, SOUTH AFRICA

SUPERVISOR : DR PE DLAMINI
CO-SUPERVISOR : MR M GXASHEKA

2020
Declaration

I declare that the mini-dissertation hereby submitted to the University of Limpopo, for the degree of Master of Science in Agriculture (Pasture Science) has not previously been submitted previously by me for a degree at this or any other university; that it is my work in design and in execution, and that all materials contained herein has been duly acknowledged

______________________________  ___________________
Mogashoa RE (Miss)  Date
Dedication

I dedicate this dissertation to my mother Rebecca Mogashoa and sister Makgomo Mogashoa.
Acknowledgments

- I would like to thank the almighty God for the knowledge and strength during the period of my study.
- Special thanks to my supervisors’ Dr PE Dlamini and Mr M Gxasheka for their time, support, comments and guidance throughout the period of study.
- To my fellow research mates Tumisho Ntsoane, Pertunia Maenetsa and Charlotte Rabopape for data collection and moral support.
- Special thanks to the soil science team (Abel Masotla, Rebone Mashapa and Millicent Khumalo) for their assistance in soil data collection and analysis.
- To the University of Limpopo Department of Plant Production, Soil Science and Agricultural Engineering for giving me the opportunity to pursue my studies.
- Special thanks to my sister Makgomo Mogashoa for her support, encouragement and motivation throughout my studies.
- Words of appreciation to my mother, aunts (Vivian Gafane and Betty Mapheto), grandmothers (Regina Gafane and Joyce Lesibe) and my friend Mmakgomo Moswedi for their encouragement throughout the period of this study.
Table of Contents

Declaration ........................................................................................................................................... i
Dedication........................................................................................................................................... ii
Acknowledgments ................................................................................................................................. iii
List of appendices ................................................................................................................................ x
Abstract............................................................................................................................................... xi

CHAPTER 1 ........................................................................................................................................... 1
GENERAL INTRODUCTION .................................................................................................................... 1
  1.1 Background .................................................................................................................................. 1
  1.2. Problem statement ...................................................................................................................... 2
  1.3. Rationale ................................................................................................................................... 2
  1.4. Purpose of the study ................................................................................................................... 3
    1.4.1. Aim ...................................................................................................................................... 3
    1.4.2. Objectives ........................................................................................................................... 3
    1.4.3. Research questions .............................................................................................................. 3

CHAPTER 2 ........................................................................................................................................... 7
LITERATURE REVIEW ............................................................................................................................. 7
  2.1. Introduction ............................................................................................................................... 7
  2.2. Global drivers of bush encroachment ......................................................................................... 7
    2.2.1. Climate ............................................................................................................................... 7
    2.2.2. Soil type ............................................................................................................................ 9
    2.2.3. Atmospheric carbon dioxide (CO₂) .................................................................................... 9
  2.3. Local drivers of bush encroachment .......................................................................................... 9
    2.3.1. Overgrazing ....................................................................................................................... 9
    2.3.2. Fire suppression .................................................................................................................. 10
    2.3.3. Soil water content ............................................................................................................... 11
  2.4. Effect of bush encroachment on herbaceous biomass production ......................................... 11
  2.5. Bush encroachment effect on herbaceous plant diversity .......................................................... 11
  2.6. Tree-grass interaction in bush encroached grassland ............................................................... 12
4.6.1. Effect of shrub structure on grass species composition and diversity along encroachment gradient.................................................................52

4.6.2. Relationship between vegetation parameters and soil nutrients along encroachment gradient.................................................................54

4.7. Conclusion ...........................................................................................................55

REFERENCES...........................................................................................................56

CHAPTER 5 ..............................................................................................................61

SUMMARY AND CONCLUSION ..............................................................................61
List of figures

Figure 2.1 Relationship between woody cover and mean annual precipitation in Africa (Sankaran et al., 2005) .................................................................................................................. 8

Figure 3.1. Location of the study site and photographs showing encroachment gradient spanning from open, intermediate and intensive, along the savanna rangeland soil profile representation of the shallow plinthic soil. ......................................................... 22

Figure 3.2. Distribution of (a) tree height (b) lowest browsable height (c) longest crown diameter and (d) shortest crown diameter in open, intermediate and intensive bush-encroached rangeland. Graphic is based on six plots per encroachment level, box plots, with whiskers extending from the 25th and 75th percentile, median marked with black horizontal line across the box and black horizontal broken line indicates the mean solid line indicates medians. Black dots outside the whiskers represent the outliers........................................................................................................................................... 26

Figure 3.3. Comparison of tree richness (a), Shannon-Wiener diversity (b) and Pielou’s evenness (c) indexes in open, intermediate and intensive bush encroached rangeland. The value is the mean ± standard error obtained from six plots in each encroachment level. Different superscripts above the bars indicate significant differences at P≤ 0.05. ............................................................................................................................................... 28

Figure 4.1. Photographs showing demarcation of plots and collection of herbaceous species data in the savanna rangeland ........................................................................................................ 40

Figure 4.2. Comparison of grass richness index (a), Shannon-Wiener index (b) and Pielou’s evenness index in open, intermediate and intensive bush-encroached grassland. The value is the mean ± standard error obtained from six plots in each encroachment level. Different letters above the bars indicate significant differences at P ≤ 0.05........................................................................................................................................ 44

Figure 4.3. Distribution of tree canopy area (a), above-ground biomass (b) and basal cover (c). Graphic is based on six plots per encroachment level and is depicted using box plots with whiskers extending from the 25th and 75th percentile, median marked with black horizontal line across the box. .................................................................................................................. 45

Figure 4.4. Topsoil (0-5 cm) distribution of (a) total carbon content (b) total nitrogen content (c) phosphorus (d) potassium (e) calcium and (f) magnesium in open, intermediate and intensively bush-encroached rangeland using box plots, with whiskers extending from the 25th and 75th percentile, median marked with black
horizontal line across the box and black horizontal dotted line indicates the mean. Black dots outside the whiskers represent the outliers.................. 47

Figure 4.5: Principal component analysis of selected soil properties and vegetation components along different encroachment gradients in a savanna rangeland........ 50
List of tables

Table 3.1. Woody and herbaceous plant species mean tree density, slope gradient and soil type for three encroached intensities (open, intermediate and intensive). .. 23
Table 3.2. Palatable, thorns, and relative abundance of woody plants in open, intermediate and intensive bush encroached rangeland. ........................................... 25
Table 4.1. Herbaceous species, life form, ecological status and relative abundance of grasses in open, intermediate and intensive bush encroached rangeland. .......... 43
Table 4.2. Correlation matrix of woody and herbaceous vegetation in open, intermediate and intensive bush encroached rangeland. Values in bold indicate significant difference at P≤ 0.05. ........................................................................................................ 49
Table 4.3. Result of principal component analysis of vegetation parameters and soil nutrient loadings from open, intermediate and intensive shrub-encroached grassland. ......................................................................................................................... 51
List of appendices

Appendix 1: One-way analysis of variance for grasses and trees in open, intermediate and intensive bush encroached savanna grassland.............................................................. 62
Appendix 2: One-way analysis of variance for soil properties in open, intermediate and intensive bush encroached savanna grassland.............................................................. 64
Abstract

Bush encroachment is a major problem in arid and semi-arid savannas characterized by a grass layer interspersed with a shrub stratum. Land cover change as a result of rapid proliferation of woody species in previously open rangelands alters herbaceous species and impacts soil properties. So far, little is known about the threshold at which woody plant density and cover affects herbaceous cover and the underlying mechanisms driving bush encroachment in arid and semi-arid rangelands are still debated. The objectives of this dissertation were to (1) to assess woody species composition and structure along an encroachment gradient and to explore the relationship between woody vegetation and herbaceous vegetation. (2) To determine the effect of increasing tree density and cover on grass species richness, diversity, evenness and selected soil nutrients in a bush encroached rangeland. In order to address these objectives, a semi-arid rangeland was demarcated into three encroachment gradients spanning from open to intermediate and intensive. Within each encroachment gradient six plots of 10 m x 10 m were randomly selected, whereby woody and herbaceous vegetation were assessed and soil properties determined. A discernible increase in woody species diversity and evenness was found along the transition from open to intensive bush encroached rangeland. Leguminous woody species *Vachellia* spp. and *Dichrostachys cinerea* were dominant along the bush encroachment gradient. Tree height was found to be positively correlated with long crown diameter (LCD) and short crown diameter (SCD). Furthermore, increasing tree density resulted in a 53% decline in grass species richness (GR). A decline in GR mirrored an increase in the composition of the decreaser species *Panicum maximum* (90%). Increasing woody plant density and cover also increased macro-nutrients; total carbon, nitrogen, phosphorus, exchangeable calcium and magnesium by 21%-159% in the shallow rangeland soils. Such quantitative information will assist rangeland managers to better understand the effects of varying bush encroachment intensities on herbaceous species composition, richness and soil properties in semi-arid savanna rangelands.

**Keywords:** Bush encroachment, species richness, diversity, composition, soil properties, semi-arid, savanna, rangelands.
CHAPTER 1
GENERAL INTRODUCTION

1.1 Background

Globally, rangelands cover approximately 51% of land surface area, and maintain 78% forage for livestock production (Asner et al., 2004). Over the last century bush encroachment has been observed in open-canopy grasslands (Guido et al., 2017). Bush encroachment is the increase in tree density in open-canopy savanna grassland ecosystems (Maestre et al., 2009; Maestre et al., 2016; Guido et al., 2017). The shift from open to bush encroached grasslands has been shown to be irreversible as it leads to ecological impacts on the environment (Li et al., 2016).

Savanna rangelands are affected by the gradual increase in woody plants relative to grass species. Savannas are constituted by the co-existence of trees and grasses, with increasing woody species in the ecosystem altering tree-grass interaction (Ward, 2005; Devine et al., 2017). The intensification of woody species suppresses the growth of herbaceous species replacing them with unpalatable woody species (Ward, 2005; Devine et al., 2017). According to Mureva and Ward (2016); Devine et al. (2017), the expansion of woody species is facilitated by herbivory actions, fire suppression, soil nutrients and climatic changes in an area. The rapid expansion of woody species alters the ecosystem structure leading to a reduction in species diversity and richness (Price and Morgan, 2008; Guido et al., 2017).

The shift from previously open to intensively bush encroached grasslands does not only affect the ecosystem structure, but also leads to degradation of rangelands, which negatively influence soil hydrology and nutrient availability (Liu et al., 2011; Li et al., 2016). Degradation of rangelands reduces vegetation cover, palatable grass species and soil quality leading to depletion of soil nutrients (Kassahun et al., 2008). Increasing woody species adversely affects the biological, physical and chemical properties of the soil and the surrounding biodiversity (Belayneh and Tessema, 2017). According to Fynn and O’connor (2000), rangeland degradation is driven by rainfall variability in arid and semi-arid environments which influences the change in vegetation within the system. Rangeland degradation is increasing at a faster rate thus threatening the quality of rangelands and food security (Maitima et al., 2009, Ravi et al., 2010).
Arid and semi-arid rangelands are highly vulnerable to degradation and may result in a decline in both primary and secondary productivity of savanna grasslands (Fynn and O’connor, 2000).

1.2. Problem statement

In South Africa, bush encroachment is a serious environmental problem (Smit, 2004). Encroachment of shrubs and trees is influenced by several factors ranging from climate, overgrazing and reduced fire intensity (Roques et al., 2001; Smit, 2004; Mussa et al., 2016). The increase in bush densities has led to a decline in grazing capacity of rangelands. Furthermore, increases in atmospheric carbon dioxide (CO₂), result in the increase of C₃ woody species at the expense of C₄ grass species and this in turn affects species composition, biomass and species diversity (Smit, 2004). Some studies (Fynn and O’connor 2000; Maitima et al., 2009), have revealed that overutilization of herbaceous plant species result in a decline in grassland productivity and subsequently promotes degradation of rangelands (Smit and Rethman, 1999). As a result of degradation of rangelands, soil physical and chemical properties are negatively affected leading to a decline in primary productivity (Belayneh and Tessema, 2017). Encroachment of woody species in rangelands is a major concern for land managers as it is considered to be a major threat to the viability of livestock enterprises (Eldridge and Solivers, 2015).

1.3. Rationale

Environmental change caused by the encroachment of woody species into open rangeland changes the availability of resources (i.e. nutrients, moisture and light) thus suppressing development of herbaceous species within an area (Guido et al., 2017). Rangelands are a major source of forage for grazing herbivores and provide great economic, social, cultural and biological values (Belayneh and Tessema, 2017). Ringrose et al. (2002) reported that semi-arid rangelands are more prone to degradation, which may further result in the establishment of trees and shrub. Little is known about the interaction between tree and grass cover as a result of rangeland degradation and the mechanisms driving bush encroachment are less clear. Bush encroachment also leads to a loss of agricultural land, which is measured by the extensive decline in the production of herbaceous species (Kraaij and Ward, 2006). It is therefore crucial to implement prudent land management practices such as keeping
correct livestock rates to ensure balance in species composition and to mitigate deterioration of rangelands.

Gómez-Rey et al. (2013) reported that increasing woody density does not only affect the total carbon (C) in bush encroached grasslands. Increasing woody density also contributes in the accumulation of soil organic carbon (SOC). Carbon enrichment in dry savannas promotes an increase in woody species through water use efficiency when water availability is a limiting factor for tree growth (Devine et al., 2017). Therefore, this study seeks to determine the effect of bush encroachment on plant diversity and selected soil properties.

1.4. Purpose of the study

1.4.1. Aim

The project aims to investigate the impact of bush encroachment on herbaceous vegetation and selected soil properties in a savanna rangeland.

1.4.2. Objectives

   a) To assess woody species composition and structure along an encroachment gradient.

   b) To determine the effect of increasing tree density on grass species richness, diversity, evenness and soil nutrients in a bush encroached rangeland.

1.4.3. Research questions

   a) How does the increase in woody density affect woody vegetation composition and structure?

   b) To what extend does tree density impact on herbaceous species composition, diversity and soil nutrients?
REFERENCES


2.1. Introduction

Increase in woody species in savannas has been evident over the last century (Moleele and Perkins, 1998; Devine et al., 2017). Savanna grasslands are dominated by trees and grasses (Wiegand et al., 2006). The phenomenon of increasing woody species across savannas is known as bush encroachment (Liu et al., 2011; Devine et al., 2017). Bush encroachment is facilitated by climatic changes, overgrazing, atmospheric carbon dioxide and fire suppression (Devine et al., 2017). These factors alter the grassland structure by promoting the suppression of grass species and supporting the establishment and growth of woody species. Changes in vegetation structure enhances the growth of undesirable and unpalatable plants at the expense of palatable herbaceous species (Moleele and Perkins, 1998), leading to modification in primary productivity, carrying capacity for grazers and nutrient availability in rangelands (Guido et al., 2017).

2.2. Global drivers of bush encroachment

2.2.1. Climate

Climate is major factor affecting ecological structure of rangelands, especially in semi-arid grasslands (Báez and Collins, 2008; Chen et al., 2015). According to Bond et al. (2003), climatic conditions (rainfall and temperature) facilitate vegetation distribution. The influence of continuous and frequent rainfall increases tree densities overtime (O’connor et al., 2014). Furthermore, Chen et al. (2015) reported that climate controls the expansion of shrublands in China, whereby woody species were found to influence the growth of herbaceous species in grasslands. Precipitation had a major influence on species richness and productivity in the savanna grassland (Chen et al., 2015). Precipitation is a defining characteristic of bush encroachment in semi-arid savannas. According to Chen et al. (2015), an increase in precipitation (rainfall) promotes an increase in density and height of woody vegetation as was evident in Australia and South Africa. Furthermore, the interaction of woody and herbaceous species is mainly controlled by climatic factors (Chen et al., 2015).
The availability of water is the determining factor in the increase in woody plant species. Mean annual precipitation is directly proportional to an increase in woody plants, thus an increase in MAP leads to an increase in woody plant species. As shown in Figure 2.1, increases with MAP from 100 mm to a threshold of 650 mm results to maximum woody cover (Sankaran et al., 2005). As MAP exceeds the threshold of 650 mm MAP woody cover is constant and further declines with increasing MAP. Devine et al. (2017), reported that MAP of 2000 mm in wet savannas has a slight effect on the expansion of woody species.

![Figure 2.1 Relationship between woody cover and mean annual precipitation in Africa (Sankaran et al., 2005).](image-url)
2.2.2. Soil type

Woody patches in savanna grasslands are associated with soil type, increased soil moisture and nutrients (Devine et al., 2017). The accumulation of nutrients in a bush encroached system creates fertility islands (Wiegand et al., 2005). The occurrence of woody species increases leaf litter and fixes nitrogen (N) which improves soil quality. In low rainfall savanna grasslands with nutrient-rich soils, the growth of palatable grasses is increased and utilization by livestock increases, thus maintaining the savanna ecosystem (Devine et al., 2017). According to Wiegand et al. (2005), bush encroachment is likely to occur in areas with shallow soils which allow the separation of roots. However, root separation in shallow soils is still poorly understood. Some studies have reported that woody species require deeper soils due to their long roots which are dependent on underground water (Adams, 1967; Britz and Ward, 2007).

2.2.3. Atmospheric carbon dioxide (CO₂)

Atmospheric CO₂ concentration facilitates the growth and functioning of plants, which is known to increase woody plant cover. Industrialization has increased atmospheric CO₂ from 277 ppm to 397 ppm in 2013 (O’connor et al., 2014). According to Archer et al. (2017), increased CO₂ concentrations restrict photosynthesis by C₃ grasses and this favours C₃ woody plants. An increase in CO₂ increases photosynthetic rates of woody species by 30-50% than in grasses (Eamus and Palmer, 2007). Woody plant species establish rapidly due to increased root biomass enhanced by greater CO₂ enrichment.

2.3. Local drivers of bush encroachment

2.3.1. Overgrazing

Overgrazing is the continuous utilisation of forage species occurring in rangelands, which over time results in a decline in biomass production (Eldridge et al., 2011). Most studies have identified overgrazing as a driving factor of bush encroachment (Archer et al., 2017; Sankaran et al., 2008; van Auken, 2009). Overgrazing leads to a decline in biomass production, grass vigour, and species richness decreases as an area becomes encroached (van Auken, 2009; Mureva and Ward, 2016). The excessive removal of herbaceous vegetation due to overgrazing promotes a decline in species diversity and basal cover resulting in a decrease in primary productivity of rangelands.
Heavy grazing changes species composition resulting in an increase in annual grass species at the cost of perennial grass species. According to Tessema et al. (2011), the increase in annual grass species promotes the establishment of unpalatable species and bare soil patches. Under normal grazing conditions the utilisation of grasses can reduce aboveground biomass and regrowth can be gained fast (van Auken, 2009). Prolonged periods of heavy grazing leads to the depletion of soil nutrients which in turn result in a decline in biomass productivity (van Auken, 2009). Also, heavy grazing depletes aboveground and belowground herbaceous biomass reducing the ability of plants to regrow. According to van Auken (2009), this favours the establishment and growth of woody species.

Overgrazing has also been reported to lead to an increase in unpalatable woody species at the expense of palatable herbaceous vegetation (Ward, 2005; Reed et al., 2015). Moreover, Smit (2004) reported that increased stocking rates promotes the reduction of growth and reproductive rate of herbaceous species thus influencing competition among different plants species. According to Blaum et al. (2007), the effect of bush encroachment due to overgrazing does not only affect rangeland carrying capacity, but it also leads to habitat loss and deterioration of rangelands. According to Wiegand et al. (2006), heavy grazing reduces grassroots, which reduce extraction of water from the topsoil and increases availability of water for woody plants in the subsoil.

2.3.2. Fire suppression

Fire suppression is a reduction in frequency and intensity of natural fire regimes (O’connor et al., 2014). Fire suppression promotes the establishment of woody plant species. Excluding fire regimes for prolonged periods results in wet savannas changing to forests (Devine et al., 2017). Fire has the ability to reduce plant biomass depending on the frequency and intensity (Higgins et al., 2000). Fire intensity is dependent on grass fuel load. The level of grass fuel load will result on the impact the fire would have on woody species (Higgins et al, 2000). Intense fires are capable of reducing woody canopies to an acceptable height for browsing animals in arid savannas (Trollope, 1974). Fire is effective in suppressing the growth of woody species while benefiting the establishment and growth of grasses (Trollope, 1974; Roques et al., 2016). According to Smit (2004), the frequent utilisation of fire or total
exclusion of fire enhances the establishment of more woody species thus promoting encroachment by bushes. Therefore, establishment of correct fire intervals may reduce the establishment and growth of woody species (Trollope, 1974). Variability in fire intensity prevents trees to develop fire-resistance, whereby most woody plant species become susceptible to fire (Higgins et al. 2000; Mureva and Ward, 2016).

2.3.3. Soil water content

The productivity in vegetation promotes increased rates of soil water utilization, leading to a decline in stored soil water (Wang et al., 2012). The replacement of soil perennial species with annual species raises the water table (Wang et al., 2012). Woody species require water and nutrients for growth and changes in evapotranspiration leads to increased utilization of underground water (Grygoruk et al., 2014). For instance, in a mire meadow in Poland with shallow ground water, bush encroachment led to increased consumption of underground water leading to declining levels of underground water levels (Grygoruk et al., 2014). According to Maestre et al. (2009); Archer et al. (2017), increasing woody plants may result in changes in the infiltration characteristic of the soil. It has been revealed that bush encroachment increases the infiltration rates and leads to a decline in evapotranspiration (Groengroeft et al., 2018).

2.4. Effect of bush encroachment on herbaceous biomass production

The shift from open savanna ecosystems to bush encroached ecosystems negatively influences the production of herbaceous biomass (van Auken, 2009). According to Keno and Suryabhagavan (2014), the increasing density of woody species result in reduction of biomass production which in turn decreases food security and affects livestock enterprises. Encroachment of woody plants affects the carrying capacity of rangelands consequently affecting livestock management. An increase in bush encroachment does not only lead to a decline in herbaceous species, but also bare patches that promote soil erosion (Moleele et al., 2002; Lesoli et al., 2013).

2.5. Bush encroachment effect on herbaceous plant diversity

Globally, encroachment of woody species has resulted in the loss of biodiversity leading to a shift in species composition (Wright et al., 2013). Land cover transformations such as bush encroachment increase resource availability, which
promotes changes in diversity of species within a rangeland (Tews et al., 2004; Guido et al., 2017). The development of woody C$_3$ plants has ecologically altered the structure of arid and semi-arid regions at the expense of C$_4$ plants. (Smit, 2004; Báez and Collins, 2008).

Increasing woody vegetation promotes loss of valuable herbaceous species, which gradually affects the functioning of the savannas. The increase in plant diversity is also influenced by an increase in carbon dioxide (CO$_2$) and nitrogen (N) deposition in soils.

2.6. Tree-grass interaction in bush encroached grassland

Trees have both negative and positive impact on grasses under tree canopies and inter-canopy spaces. Increase in woody species enhance soil nutrients leading to a decline in evapotranspiration and an increase productivity of grasses (Belsky, 1994; Moustakas et al., 2010). According to Scholes and Archer (1997), under canopy of woody plant species there is an increase in organic matter, water availability and a decline in soil temperatures which leads to an increase in herbaceous species productivity. Rignos et al. (2009) revealed that within enclosures created by woody species herbivory movement is reduced therefore, the establishment and growth of herbaceous plants species is facilitated. Woody species are facilitated by availability of resources in an area. Grasses provide a conducive environment for the growth of woody plants through decomposition of grass litter which improves fertility status of the soil and water holding capacity of the soil (Archer et al., 2017).

2.7. Bush encroachment effect on selected soil properties

Spatial heterogeneity of soil resources often occurs in savanna ecosystems. The difference in soil resources affects the diversity and productivity of rangelands (Eldridge et al., 2011). Heterogeneity in soil nutrients has the ability to cause a decline in primary productivity of plant species (Eldridge et al., 2011). Bush encroachment changes the distribution of soil resources and thus alters vegetation structure and distribution (Li et al., 2008). This promotes the development of bare patches leading to soil erosion (Eldridge et al., 2011). According to Doetterl et al. (2016), erosion leads to the loss of organic matter through increased decomposition and the removal of organic matter. Bare patches within a savanna grassland are exposed to direct sunlight, subsequently increasing the soil temperature and retarding organic nitrogen
(N) incorporation thus leading to denitrification and volatilization of ammonia (Eldridge et al., 2011).

According to Yusuf et al. (2015), carbon (C) and nitrogen (N) in grasslands are dependent on rainfall. A study conducted by Yusuf et al. (2015), reported that areas that receive < 280 mm rainfall per annum resulted in increased soil C and N while areas receiving > 600 mm rainfall per annum had a decrease in soil C and N in bush-encroached areas. According to DeMarco et al. (2016), bush encroachment increased C under tree canopies. The increase in soil C is facilitated by woody and herbaceous plant species occurring beneath woody species (DeMarco et al., 2016). Throop and Archer (2008) conducted a study at Santa Rita Experimental Range, which reported that fertility islands promote by the accumulation of C and nutrients in the soil of in bush encroached grasslands. Fertility islands are landscapes with unfertile areas that are separated by nutrient rich soils with woody plants (Ridolfi et al., 2008). Throop and Archer (2008), reported that soil carbon stocks depend on the population of woody plant species, size and structure.
REFERENCES


CHAPTER 3

ASSESSMENT OF WOODY PLANT COMPOSITION, STRUCTURE AND PLANT DIVERSITY ALONG BUSH ENCROACHMENT GRADIENTS IN SAVANNA RANGELANDS

Abstract

The objectives of this study were to assess woody species composition and structure along an encroachment gradient and to explore the relationship between woody vegetation and herbaceous vegetation. The grassland was demarcated into three encroachment intensities ranging from open to intermediate and intensive. Within each encroachment intensity six plots of 10 m x 10 m were randomly selected, from which tree species were identified. The height of the tree, long crown diameter, short crown diameter and lowest browsable height of all tree species were measured. There was a significant increase in tree species diversity and evenness from open to intensive bush encroached rangeland. The study site was dominated by leguminous woody species *Vachellia* spp. and *Dichrostachys cinerea*. Tree height was positively correlated with long crown diameter (LCD) and short crown diameter (SCD). Bush encroachment affected grass species composition and created enclosures in previously open grasslands. The study also revealed that an increase in woody species leads to an increase in woody canopy area and above ground biomass, while a marginal decline in basal cover occurred with increasing woody plant cover.

**Keywords**: Bush encroachment, woody species richness, diversity, evenness, *Dichrostachys cinerea, Vachellia* species
3.1. Introduction

Woody plants are perennial plants (i.e. trees and shrubs), which produce wood as their structural tissue (Götmark et al., 2016). In most savannas, woody plants form the most important vegetation components of the ecosystem after grasses. Woody plants are known to provide forage, shade and shelter for animals (Lesoli et al., 2013). Savanna rangelands deteriorate due to proliferation of woody plants at the expense of grasses in many arid and semiarid regions (Moleele and Perkins, 1998; Ward, 2005). This process is locally known as bush encroachment (Trollope et al., 1989; Ward, 2005).

In arid and semiarid regions, woody species have both negative and positive effect on the life forms occurring in their understory and surrounding areas (Archer et al., 2017). Over a period of time woody plants become invasive and facilitate bush encroachment in semi-arid rangelands (Belayneh and Tessema, 2017). Bush encroachment in savanna rangelands is established via transformation of the savannas to dense woody plants characterised by lower grass cover (Meik et al., 2002; Ward, 2005). The encroaching species are often unpalatable to browsers (Kraaij and Ward, 2006) or not accessible to browsers especially when thorny (Moleele et al., 2002). In Southern Africa, approximately 13 million hectares by 1960s were exposed to bush encroachment (Trollope et al., 1989) and this phenomenon is still increasing to date.

Many studies have associated woody plant encroachment with change in fire regimes, overgrazing, soil moisture, nutrients and global climate change (Ward, 2005, Bond, 2008, van Auken, 2009). The long-term absence of fire increases woody plant encroachment by enabling woody plant seedlings and saplings to develop to fire resistant stages (Trollope, 1980, Bond et al., 2003). Overgrazing leads to the depletion of herbaceous species (Angassa and Oba, 2010; Devine et al., 2017), allowing competition among grasses and woody species. Herbaceous species utilise soil water in the topsoil, and water in the subsoil becomes available for woody plants (Wiegand et al., 2005). The occurrence of overgrazing enhances woody plant growth. According to Scholes and Archer (1997), the increase in woody species leads to competition, which promote self-thinning, therefore, modifying woody species dominating in an area. The competition of trees in previously open rangelands also facilitates the suppression of other woody plants in the area (Scholes and Archer, 1997). However,
little is known about tree-tree interaction mechanisms especially in semi-arid savanna grasslands.

There is little information available regarding woody structure and diversity of encroaching woody plants. Understanding woody plant structure is essential for effective management of savanna rangelands. Tefera et al. (2008) indicated that planning of control measures requires quantitative data on species composition, density and height distribution of woody plants. Therefore, the objective of this study was to assess woody species composition and structure along a bush encroachment gradient.

3.2. Methodology

3.2.1. Site description

The site is located at the University of Limpopo Syferkuil Experimental farm in the Capricorn District Municipality, Limpopo Province, South Africa (S25° 50', E29°42'). The study area experiences an arid steppe hot climate with distinct dry season, and receives rainfall ranging from 400 to 600 mm per annum, the majority of which falls during the summer months (November and March) and mean annual temperatures ranging from 4 to 27°C (Munjonji et al., 2016). The site is located on a relatively flat (0-2%) landscape position, with an altitude that ranges from 1234 to 1240 m above sea level (Table 3.1.). The dominant soil at the site is a shallow, moderately acidic, yellowish brown and sub-angular blocky Westleigh soil form characterized by an Orthic A horizon limited by soft plinthic B horizon (Soil Classification Working Group, 1991) or Plinthic (IUSS Working Group WRB, 2014).

The research was conducted in a 19.8 ha bush encroached savanna camp used for livestock grazing. The grazing camp has been used by the university for summer grazing and rested in winter for the last 30 years. The vegetation type in the study area was defined as Polokwane Plateau Bushveld (Mucina and Rutherford, 2006). Natural succession and grazing have been the main factors determining vegetation development in the savanna rangeland. The tree layer consists of Vachellia (Acacia) hebeclada, V. Karoo, V. tortillis, Aloe ferox, Dichrostachys cinerea, Mimusops caffra, Opuntia ficus indica and Ziziphus mucronata. The grass species layer entails Arista congesta, Brachiaria nigropedata, Cynodon dactylon, Digiteria eriantha, Eragrostis lehmanniana, Eragrostis rigidior, Eragrostis superba, Heteropogon contortus, Melinis
repens, Panicum maximum, Panicum natalense, Pogonarthria squarossa, Schmidtia pappophoroides.

3.2.2. Research design

Owing to the study being on the same soil type (Westleigh) and topography (gentle), bush encroachment gradient that captures transitional zones spanning from open to intermediate and intensive encroached rangeland were identified and characterised by quantification of tree density (number of trees per 100 m²) (Table 3.1; Figure 3.1). In each identified bush encroachment level, six plots of 10 m x 10 m were randomly selected, from which woody plant structure and species composition were determined.

Figure 3.1. Location of the study site and photographs showing encroachment gradient spanning from open, intermediate and intensive along the savanna rangeland as well soil profile of the shallow plinthic soil.
Table 3.1. Woody and herbaceous plant species mean tree density, slope gradient and soil type for three encroached intensities (open, intermediate and intensive).

<table>
<thead>
<tr>
<th>Intensity</th>
<th>TD</th>
<th>Location (m)</th>
<th>Slope (%)</th>
<th>Soil</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>E29°41,974’</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>E29°42,008’</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>E29°41,948’</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
3.3. Data collection

All woody species occurring within each plot per bush encroachment level were counted and identified. The plant height, LBH, long and short crown diameter of the woody species were measured and recorded. Plants > 2m were measured by using a step ladder.

Tree canopy area (TCA) was calculated from the canopy diameter using the formula following Tessema et al. (2017) and Hesselbarth et al. (2018).

\[ TCA = \left( \frac{d_1 \times d_2 \times \pi}{4} \right) \]

Where \( d_1 \) is the longest crown diameter and \( d_2 \) is the shortest crown diameter.

Species richness in each bush encroached intensity was estimated using the Menhinick’s index (Magurran, 2004), which is calculated as follows:

\[ D = \frac{S}{\sqrt{N}} \]

Where \( S \) is the number of different species represented within each encroachment intensity and \( N \) is the total number of species in each encroachment intensity.

Species diversity in each bush encroached level was estimated using the Shannon-Wiener diversity index (Magurran, 2004), which is calculated as follows:

\[ H = -\sum_{i=1}^{S} (P_i \ ln P_i) \]

Where \( H \) is the Shannon-Wiener index (the measure of species diversity), \( P_i \) is the weight proportion of total number of species, \( ln \) is the natural log of the total number of species, \( S \) is the number of species in the each encroachment level. Typical values for Shannon-Wiener diversity index range between 1.5 and 3.5 in most ecological studies (Magurran, 2004).

Furthermore, species evenness in each bush encroached level was estimated using the Pielou’s evenness index (Magurran, 2004), which is calculated as follows:

\[ J = \frac{H}{lnS} \]

Where \( H \) is the Shannon-wiener diversity index, \( ln \) is the natural log and \( S \) is the total number of species in each encroachment intensity.
3.4. Statistical analysis

Descriptive statistics such as mean, maximum, minimum and coefficient of variation (CV) of species composition and plant diversity were computed in Microsoft Excel. The vegetation and soil data were subjected to analysis of variance (ANOVA) using SAS PROC GLM (SAS version 9.4). When ANOVA effect was significant, mean separations were performed using the Tukey test at $P \leq 0.05$.

3.5. Results

In this study, we found eight tree species along the bush encroachment gradient (Table 3.2). The tree layer in open rangeland was dominated by *V. hebeclada* (36%), followed by *V. karoo* (33%) and *Opuntia ficus indica* (24%). The intermediate bush-encroached rangeland was dominated by *Aloe forex* (32%), followed by *V. tortillis* (24%), *Opuntia ficus indica* (21%) and *V. hebeclada* (13%), while the intensive bush-encroached rangeland was dominated by *V. hebeclada* (41%), *Dichrostachys cinerea* (39%) and *V. karoo* (18%).

Table 3.2. Palatable, thorns, and relative abundance of woody plants in open, intermediate and intensive bush encroached rangeland.

<table>
<thead>
<tr>
<th>Species</th>
<th>Palatability</th>
<th>Presence of Thorns</th>
<th>Open</th>
<th>Intermediate</th>
<th>Intensive</th>
<th>Relative abundance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Vachellia hebeclada</em></td>
<td>+</td>
<td>+</td>
<td>36</td>
<td>13</td>
<td>41</td>
<td></td>
</tr>
<tr>
<td><em>Vachellia Karoo</em></td>
<td>+</td>
<td>+</td>
<td>33</td>
<td>4</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td><em>Vachellia tortillis</em></td>
<td>+</td>
<td>-</td>
<td></td>
<td>24</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td><em>Aloe ferox</em></td>
<td>+</td>
<td>+</td>
<td></td>
<td>32</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td><em>Dichrostachys cinerea</em></td>
<td>+</td>
<td>+</td>
<td>3.6</td>
<td>2</td>
<td>39</td>
<td></td>
</tr>
<tr>
<td><em>Mimusops catfra</em></td>
<td>+</td>
<td>-</td>
<td></td>
<td>4</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td><em>Opuntia ficus indica</em></td>
<td>+</td>
<td>+</td>
<td>24</td>
<td>21</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td><em>Ziziphus mucronata</em></td>
<td>+</td>
<td>+</td>
<td>3.4</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

Note: Plus (+) sign indicates palatability of woody plant. Plus (+) sign indicates presence of thorns and a minus (-) indicates absence of thorns. Minus (-) indicates absence of woody plant.

Tree height, lowest browsable height, longest and shortest crown diameter increased with increasing encroachment intensity at the site (Figure 3.2 a-d), and were significantly different at $P<0.05$ (Appendix 1). The average tree height increased from
0.76 m in open to 1.14 m in intermediate and 3.25 m in intensive bush encroached rangeland. Lowest browsable height was similar between open (0.17 m) and intermediate (0.17 m) and increased to 0.95 m in intensive bush encroached rangeland. Longest crown diameter varied little between open (1.35 m) and intermediate (1.52 m) and increased to 2.26 m in intensive bush encroached rangeland. Similarly, shortest crown diameter varied little from 1.07 m to 1.18 m in open and intermediate, respectively and increased to 1.86 m in intensive bush encroached rangeland (Figure 3.2 d).

Figure 3.2. Distribution of (a) tree height (b) lowest browsable height (c) longest crown diameter and (d) shortest crown diameter in open, intermediate and intensive bush-encroached rangeland. Graphic is based on six plots per encroachment level, box plots, with whiskers extending from the 25th and 75th percentile, median marked with black horizontal line across the box and black horizontal broken line indicates the
mean solid line indicates medians. Black dots outside the whiskers represent the outliers.

Tree richness index \( (P = 0.038, F = 4.093) \), Shannon-Wiener diversity index \( (P = 0.032, F = 4.353) \), and evenness index \( (P = 0.023, F = 4.986) \) varied significantly along the bush encroachment gradient (Figure 3.3; Appendix 1). Tree species richness varied along the three encroachment gradients, with a significant decline in species diversity from open to intermediate and from intermediate to intensive bush encroached rangeland. The Shannon-Wiener diversity index increased significantly from intermediate to intensive bush encroached rangeland. Species evenness index increased significantly with the increase in species diversity from intermediate to intensive bush encroached rangeland (Appendix 1).
Figure 3.3. Comparison of tree richness (a), Shannon-Wiener diversity (b) and Pielou’s evenness (c) indexes in open, intermediate and intensive bush encroached rangeland. The value is the mean ± standard error obtained from six plots in each encroachment level. Different superscripts above the bars indicate significant differences at $P \leq 0.05$. 

28
3.6. Discussion

3.6.1. Woody plant composition along encroachment gradient

In this study, woody species composition increased along the encroachment gradient varying from open to intermediate and intensive. The encroachment in the study site was mostly driven by palatable thorny woody plants (Table 3.2). The study area was dominated by *Vachellia* species in the open and intensive bush encroached rangeland. Previous studies (O'Connor and Crow, 1999; Ward, 2005; Tokozwayo, 2016) also reported dominance of *Vachellia* species in bush encroached rangelands. The transitional zone being the intermediate bush encroached rangeland was dominated by the thorny *Aloe ferox* species, while *Dichrostachys cinerea* had a major contribution in the intensive bush encroached rangeland. Woody species increased with overgrazing observed to occurring at the study site. In line with this study, Jordaan (2010) in a Sourish bushveld reported that *D. cinerea* and *Vachellia* species were the first to establish and they tend to increase overtime. In a study by Roques *et al.* (2001), increasing woody species in the Lowveld savanna of north-eastern Swaziland was dominated by the leguminous species *D. cinerea* contributing about 81%. The high grazing pressure in that area led to the increase in woody plant species. A study Breebaart *et al.* (2002) reported that *Acacia* and *Aloe* species are utilised by browsing animals during winter. This study revealed that grazing animals utilise the leaves of the succulent *Aloe* species (*Aloe ferox, Aloe maculata*). In the current study, it has not been established whether the animals grazed the *Aloe ferox* species found at the site.

3.6.2. Woody structure and diversity along encroachment gradient

This study revealed that woody plant height, lowest browsable height and canopy diameters increased linearly from open to intensive bush encroached rangeland (Figure 3.2 a-d). The increase of tree height with increasing encroachment intensity at the study site may depict transitional stages of bush encroachment within the study site. A study by Joubert *et al.* (2008) explained that the dominance of smaller trees characterizes the transition state while larger trees characterize a heavy encroached state. Previous studies (Strohbach and Petersen, 2007; Shackleton and Gambiza, 2008; Gxasheka, 2013) also observed small trees or seedlings on non-encroached sites and larger trees on encroached sites. The study observed higher lowest browsable height (>1.5 m) on intensive encroached rangeland. This implies that most
of trees occurring on the intensive encroached rangeland were not available for livestock browsing. Most browsing livestock are only able to utilize trees from the ground up to 1.5 m in height (Breebaart et al., 2002; du Plessis et al., 2004). The study observed an increase in canopy diameter in the intensive encroached rangeland. The results of this study agree with previous studies (Meik et al., 2002, Karuaera, 2011, Gxasheka, 2013), who found greater canopy diameter and cover under intensive encroached sites. Woody plants with larger canopy diameters usually have intact canopies, with reduced interspace between the canopies. This phenomenon prevents solar radiation and rainwater infiltration which in turn affects grass species composition under trees and availability of herbaceous vegetation between the canopies (Belay and Moe, 2015).

In this study, Shannon-Wiener diversity of trees was not significantly different between open and intensive encroached rangeland. Similar results have been reported for bush encroached savanna rangelands in Southern Oromia National Regional State, Ethiopia, where tree Shannon-Wiener diversity was not significantly different between non-encroached and encroached rangeland (Gobelle and Gure, 2018). In this study species richness declined significantly from open to intermediate bush encroached rangeland. Species richness further increased significantly from intermediate to intensive bush encroached rangeland. This finding shows that bush encroachment increases woody plant species richness. A previous study by Gobelle and Gure (2018) also reported higher tree species richness in intensive encroached rangelands.

3.7. Conclusion

In this study bush encroachment was driven by Vachellia species and D. cinerea in the study site. Increasing woody species increase tree height and lowest browsable height, which limits the availability of the woody species for browsing animals. Encroachment of woody species also led to a significant increase in species diversity and evenness along the encroachment gradient. Further studies will focus on evaluating possible techniques for management of woody plants in the bush encroached rangeland.
REFERENCES


Karuaera, N.A.G, 2011. Assessing the effects of bush encroachment on species abundance, composition and diversity of small mammals at the neudamm agricultural farm, khomas region, Namibia. MSc Dissertation. University of Namibia, Namibia.


CHAPTER 4
EFFECT OF BUSH ENCROACHMENT ON HERBACEOUS VEGETATION AND SELECTED SOIL PROPERTIES IN A SAVANNA RANGELAND

Abstract
Bush encroachment, which occurs at different rates and densities is a serious challenge in semi-arid savannas characterised by co-dominance of shrubs and grasses. Mechanisms driving bush encroachment in savannas are varied and complex, and the thresholds of tree canopy cover discernibly affecting herbaceous vegetation and soil nutrients are less understood. In this study, we quantified the effect of increasing tree canopy cover and density along a bush encroachment gradient spanning from open to intermediate, transitioning to intensive encroached grassland on herbaceous vegetation and soil nutrients in a savanna grassland sited on a shallow loamy plinthic soil. Results showed that an increase in tree density and cover from a threshold of 800 trees ha\(^{-1}\); 1.9 m\(^2\) in open to 1700 trees ha\(^{-1}\); 3.1 m\(^2\) in intensive bush-encroached grassland resulted in 53% decline in grass species richness (GR). Along the encroachment gradient, there was considerably a stronger negative association between GR and tree height \((r = -0.83)\). A decline in GR in the intensive bush-encroached grassland was mirrored by an increase in composition of *Panicum maximum* (90%), a shade-tolerant decreaser II species. Increasing tree canopy cover led to an increase (21%-159%) in total carbon, nitrogen, phosphorus, exchangeable calcium and magnesium in the surface soil of the bush encroachment gradient. The study provides improved understanding of the relationship between tree canopy cover and grass diversity as well as associated soil nutrients in a progressing bush encroachment gradient of a savanna rangeland. This is a necessary step to improve rangeland management and to mitigate the impacts of further shrub invasion.

**Keywords:** bush encroachment, grass species composition, richness, diversity, soil nutrients, savanna, *Vachellia* species and *Dichrostachys cinerea*
4.1. Introduction

Savannas, characterised by highly heterogeneous co-dominance of woody plants (shrubs and trees) and grasses (Scholes and Archer, 1997; Moustakas et al., 2010; Sankaran et al., 2004) are rapidly transitioning into shrub or tree-dominated landscapes (Wilcox et al., 2018). The tree-grass mixture in savannas result in structural variation imposed by a discontinuous canopy cover (Holdo and Mack, 2014) is considered one of the most threatening forms of rangeland degradation (Briggs et al., 2005; Li et al., 2016). The Millennium Ecosystem Assessment Desertification Synthesis document supported by the United Nations aimed at informing national and international policies, advocates that bush encroachment is indeed a major ecological expression of degradation (Maestre et al., 2009). Bush encroachment is reported to be acute in arid and semi-arid savanna grasslands characterised by shallow soils limited by depth and availability of water (Wiegand et al., 2005).

The establishment of trees or shrubs in rangelands represents an extensive land cover change that alters ecosystem structure and soil processes (Nunes Biral et al., 2019). The rapid expansion of woody plants into formerly open rangelands leads to a decline in species diversity, richness and evenness; major components of biodiversity (Price and Morgan, 2008; Guido et al., 2017). Transitions from grass-to-shrub-dominated rangelands, not only influence vegetation structure, but also influence the spatial distribution and cycling of soil carbon and nutrients (Li et al., 2016; Belayneh and Tessema, 2017; Turpin-Jelfs et al., 2019). In shallow soils under arid and semi-arid grasslands, surface carbon and nutrient pools are particularly dynamic in response to shrub encroachment (Throop and Lajtha, 2018).

Mechanisms allowing co-dominance of trees and grasses in savannas are still debated (Sankaran et al., 2004; Moustakas et al., 2010), and those promoting expansion of bush encroachment have not been fully identified (Thompson et al., 2017). Increasing woody species into previously open savannas alters tree-grass interactions (Devine et al., 2017). Yet, little is known about the interactions between trees and grasses, especially in semi-arid savanna grasslands sited on shallow soils (Belsky et al., 1989; Wiegand et al., 2005; Belayneh and Tessema, 2017). Another key remaining challenge is to understand the relative contribution of tree canopies and grasses on soil nutrient heterogeneity (Holdo and Mack, 2014; Turpin-Jelfs et al., 2019). Changes in relative abundances of grasses and shrubs at different stages of bush
Encroachment may alter the contribution of vegetation to carbon and nutrient storage in ways not fully understood in many environments (Throop and Lajtha 2018; Wang et al., 2019). As such, an improved understanding of tree-grass interactions is necessary (Hesselbarth et al., 2018).

Bush encroachment occurs at different rates and densities within savannas. Many of the existing studies have offered little insight on the thresholds of tree canopy cover and density that affect herbaceous vegetation. For instance, Ritchter et al. (2001) investigated the effect of tree density on the grass layer of three semi-arid savannas in the Northern Cape and Northwest provinces of South Africa and found that an increase in tree density to a threshold of approximately 2500 trees ha⁻¹ did not affect grass species composition. This is because it is difficult to establish the threshold at which an increase in tree density and cover affects herbaceous vegetation and soil nutrients (Nunes Biral et al., 2019).

In South Africa, most savanna rangelands are undergoing rapid bush encroachment as a result of fire exclusion, grazing and climate change (O’Connor et al., 2014). Encroachment of woody species into previously open rangelands is a major concern for land managers as it is considered to be a threat to the viability of both communal and commercial rangelands. Bush encroachment may alter forage availability for livestock (Wiegand et al., 2005; 2006; Eldridge and Soliveres, 2014). The land cover transformation from grasslands to shrublands promotes the establishment of undesirable and unpalatable plants at the expense of palatable herbaceous species (Moleele and Perkins, 1998) leading to modification of primary productivity in rangelands (Guido et al., 2017). Increases of woody species may also suppress herbaceous plants and reduce biodiversity (Moustakas et al., 2010; Guido et al., 2017).

The present study seeks to answer the following research question. To what extent is an increase in shrub density and cover along a progressing bush encroachment influencing herbaceous vegetation and soil nutrients in shallow soil? Given the increasing evidence of intensification of bush encroachment into formerly open savanna grasslands in sub-Saharan Africa (Venter et al., 2018). It is therefore important to gain a better understanding of how a transition from open to a shrub dominated landscape affects herbaceous vegetation and belowground nutrient storage in savannas, which represent the largest biome in South Africa (Mucina and Rutherford, 2006).
The objectives of the study were to determine the effect of increasing tree density on grass species richness, diversity, evenness and soil nutrients along a bush encroachment gradient spanning from open to intermediate and transitioning into intensive shrub-encroached grassland. A better understanding of how changes in tree architecture during shrub encroachment influences understory herbaceous vegetation and inherent soil nutrients is a necessary step to improve rangeland management and to mitigate the impacts of further shrub invasion.
4.2. Methodology

4.2.1. Site description

The study site is a savanna rangeland located at Syferkuil Experimental Farm (SEF) Capricorn District Municipality, Limpopo Province, South Africa. At SEF, the experiment was conducted in a 19.8 ha in shrub-encroached savanna rangeland camp used for livestock grazing. The rangeland has been freely grazed by livestock for at least 30 years. Natural succession, grazing and fire suppression have been the main factors determining development of vegetation structure in the rangeland (Dlamini et al., 2019). For further details refer to Chapter 3, section 3.2.1.

4.2.2. Research design

A soil and vegetation survey were carried out in June 2017 winter grazing season across the shrub-encroached savanna rangeland. Vegetation parameters were investigated along a shrub encroachment gradient spanning from open to intermediate and intensive. In each encroachment level, six 10 m × 10 m plots were randomly selected and marked on the same plinthic soil type (Westleigh), with similar topography position (0-2%).

Please refer to Chapter 3, section 3.2.2 for more details.

4.3. Data collection

4.3.1. Herbaceous vegetation sampling

Within each plot, six 0.5 m × 0.5 m quadrats were used to collect herbaceous vegetation. All herbaceous species within each quadrat were identified, recorded and their tuft diameter and distance between tufts were measured using 1 m ruler. Above-ground biomass within the quadrat was harvested above 3 cm from the soil surface using grass cutting shears to allow regrowth of grass species. Grass species were arranged according to species and placed on different paper bags. The collected grass samples were oven dried at 60 °C for 48 hours to determine the above ground biomass.

Grass basal cover was estimated from average tuft diameter of individual plants (Figure 4.1.) using the following formula by Hardy and Tainton (1993):
Figure 4.1. Photographs showing demarcation of plots and collection of herbaceous species data in the savanna rangeland

\[ BC = 19.8 + 0.39 (D) - 11.87 (\log_e D) + 0.64 (d) + 2.93 (\log_e d). \quad \text{(Eq. 1)} \]

Where \( D \) is the distance to the edge of the nearest tuft (cm) and \( d \) is the tuft diameter (cm)

The diversity of trees and grasses was investigated in the study with relevance to species richness (number of species present in a plot) and their relative abundances (evenness) and the Shannon-Wiener diversity index (Magurran, 2004), which were calculated as follows.

\[ R = S \quad \text{(Eq. 2)} \]

\[ E = \frac{H}{\ln S} \quad \text{(Eq. 3)} \]

\[ H' = \sum_{i=1}^{S} (p_i \ln p_i) \quad \text{(Eq. 4)} \]
Where \( H \) is the Shannon-Wiener index (the measure of species diversity), \( p_i \) is the weight proportion of total number of species, \( \ln \) is the natural log of the total number of species.

4.3.2. Soil sampling and analyses

In each of the replicate plots per encroachment level, six intact soil samples (8 cm diameter and, 10 cm deep) were randomly collected using a core auger from the topsoil layer (0-10 cm) at interstitial areas beyond tree canopies but within the range of extension of the root zone following Belsky et al. (1989) and Simmons et al. (2008). Soils were extruded into polythene sample bags, sealed and taken to laboratory where they were air dried and passed through a 2-mm apertue metal sieve to remove visible plant material for chemical and physical soil analysis. Soil particle size distribution was determined using the hydrometer method (Bouyoucos, 1962). Dry soil was ball-milled and total C and N determined by automated Dumas dry combustion using a Leco CNS 2000 analyser (LECO Corporation, St. Joseph, MI). Soil pH was determined in a 1:2.5 solution ratio in both deionized water and 1M KCl suspension using a glass electrode. Exchangeable cations Ca and Mg were first extracted in 1M KCl, while P, K, were extracted in an Ambic 2 extractant containing 0.25M NH\(_4\)HCO\(_3\). The detection of the extracted cations was done by inductively coupled plasma optical emission spectrometry (ICP-OES) using an Optima 7300DV spectrometer (Perkin Elmer, Inc., 2 Shelton, CT).

4.4. Statistical analysis

Box plots, which characterize the sample using the minimum, lower quartile, median, upper quartile and maximum were computed to visually assess variability of vegetation and soil properties in open, intermediate and intensive bush-encroached grassland. The vegetation and soil nutrients were subjected to one-way analysis of variance (ANOVA) to determine differences along the bush-encroachment gradient. Significant mean differences (\( P \leq 0.05 \)) between bush encroachment levels were separated using Tukey. Initial analysis of the relationship between tree and grass parameters consisted of Pearson correlation analysis that was used to test the strength of the correlations between variables along the encroachment gradient sites. Correlations with \( P \leq 0.05 \) were deemed statistically significant (STATISTICA, 7.0). Principal component analysis plot, which compresses large sets of correlated multivariate data was produced from
the two highest eigenvalues (principal components) to identify relations and analyse structure among the measured vegetation parameters and inherent soil properties (Webster, 2001).
4.5. Results

Total of fourteen grass species were observed across the bush encroachment gradient (Table 4.1). In open rangeland, grass layer was dominated by *Eragrostis rigidior* (60%) and *Schmidtia pappophoroides* (18%), while the intermediate bush encroached rangeland was dominated by *Eragrostis rigidior* (24%) and *Eragrostis superba* (24%). The intensive bush encroached rangeland was dominated by *Panicum maximum* (90%).

Table 4.1. Herbaceous species, life form, ecological status and relative abundance of grasses in open, intermediate and intensive bush encroached rangeland.

<table>
<thead>
<tr>
<th>Species</th>
<th>Life form</th>
<th>Ecological value</th>
<th>Open</th>
<th>Intermediate</th>
<th>Intensive</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arista congesta</td>
<td>WP</td>
<td>Inc II</td>
<td>0.8</td>
<td>0.5</td>
<td>-</td>
</tr>
<tr>
<td>Brachiaria nigropedata</td>
<td>P</td>
<td>Dec</td>
<td>4</td>
<td>0.3</td>
<td>-</td>
</tr>
<tr>
<td>Cynodon dactylon</td>
<td>WP</td>
<td>Inc</td>
<td>4</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Digiteria eriantha</td>
<td>P</td>
<td>Dec</td>
<td>7</td>
<td>16</td>
<td>-</td>
</tr>
<tr>
<td>Eragrostis lehmanniana</td>
<td>P</td>
<td>Inc II</td>
<td>-</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Eragrostis rigidior</td>
<td>WP</td>
<td>Inc II</td>
<td>60</td>
<td>24</td>
<td>3</td>
</tr>
<tr>
<td>Eragrostis superba</td>
<td>WP</td>
<td>Inc II</td>
<td>0.2</td>
<td>24</td>
<td>-</td>
</tr>
<tr>
<td>Heteropogon contortus</td>
<td>P</td>
<td>Inc II</td>
<td>2</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>Melinis repens</td>
<td>WP</td>
<td>Inc II</td>
<td>-</td>
<td>0.7</td>
<td>-</td>
</tr>
<tr>
<td>Panicum maximum</td>
<td>P</td>
<td>Dec</td>
<td>-</td>
<td>8</td>
<td>90</td>
</tr>
<tr>
<td>Panicum natalense</td>
<td>P</td>
<td>Inc II</td>
<td>2</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Pogonarthria squarossa</td>
<td>WP</td>
<td>Inc II</td>
<td>-</td>
<td>0.3</td>
<td>-</td>
</tr>
<tr>
<td>Schmidtia pappophoroides</td>
<td>P</td>
<td>Dec</td>
<td>18</td>
<td>5</td>
<td>-</td>
</tr>
<tr>
<td>Themeda triandra</td>
<td>P</td>
<td>Dec</td>
<td>2</td>
<td>0.01</td>
<td>-</td>
</tr>
</tbody>
</table>

*Note: P-long-lived perennials, WP-Weak perennials, Inc II-Increaser II species, Dec-decreaser species, (-) indicates absence of species (Oudtshoorn, 2014).*

Grass species richness varied from open 1.39 to 1.82 and 0.66 in intermediate and intensive bush encroached rangeland, and was significant at P<0.05. As such, a decline of 53% was found from open to intensive bush encroached rangeland (Figure 4.2). Shannon-Wiener index increased by 21% from open to intermediate and
decreased by 10 % in intensive bush encroached rangeland. A marginal decline of 9% was found from open to intensive bush encroached rangeland.

Figure 4.2. Comparison of grass richness index (a), Shannon-Wiener index (b) and Pielou’s evenness index in open, intermediate and intensive bush-encroached grassland. The value is the mean ± standard error obtained from six plots in each encroachment level. Different letters above the bars indicate significant differences at \( P \leq 0.05 \).
Tree canopy area increased linearly along the encroachment gradient. With the increase in woody species above ground biomass increased from open to intensive bush encroached rangeland and basal cover declined with the increase in woody species (Figure 4.3).

Figure 4.3. Distribution of tree canopy area (a), above-ground biomass (b) and basal cover (c). Graphic is based on six plots per encroachment level and is depicted using box plots with whiskers extending from the 25th and 75th percentile, median marked with black horizontal line across the box.
Soil total C, macro-nutrients total N and P and exchangeable cations (Ca and Mg) in the topsoil layer (0-5 cm) significantly (P<0.05) increased with increasing tree density along the bush encroachment gradient (Figure 4.4 a-f; Appendix 2). Total C content increased to 8.05 g C kg\(^{-1}\) in intermediate and 14.2 g C kg\(^{-1}\) in intensive bush-encroached rangeland compared with 5.72 g C kg\(^{-1}\) in open (reference site). Therefore, in comparison to the open rangeland, bush encroachment increased total C content by 40% in intermediate and by 147% in intensive-bush encroached rangeland. Total N content was 0.37 g N kg\(^{-1}\) in open rangeland, increased by 22% to 0.45 g N kg\(^{-1}\) in intermediate and by 159% to 0.96 g N kg\(^{-1}\) in intensive bush-encroached rangeland. Compared to 3.78 mg kg\(^{-1}\) in open rangeland, P was 4.89 mg kg\(^{-1}\) in intermediate and 7.49 mg kg\(^{-1}\) corresponding to a 29% and 98% increase, respectively. Interestingly, potassium (K) increased by 20% (303.50 mg kg\(^{-1}\)) and slightly decreased by 4% in intensive bush-encroached (241.20 mg kg\(^{-1}\)) compared to 253.36 mg kg\(^{-1}\) in open rangeland.
Figure 4.4. Topsoil (0-5 cm) distribution of (a) total carbon content (b) total nitrogen content (c) phosphorus (d) potassium (e) calcium and (f) magnesium in open, intermediate and intensively bush-encroached rangeland using box plots, with whiskers extending from the 25th and 75th percentile, median marked with black horizontal line across the box and black horizontal dotted line indicates the mean. Black dots outside the whiskers represent the outliers.
In open rangeland, TH was positively correlated with TCA (r = 0.87), LCD (r = 0.70), SCD (r = 0.47), LBH (r = 0.42) and negatively correlated with GR (r = -0.97) and GSD (r = -0.84). Both LCD and SCD were negatively correlated with GR (r = -0.89-0.96) and GSD (r = -0.85-0.89), respectively. LBH was negatively correlated with TSD and TE (r = -0.89). TR was positively correlated with BC (0.93).

In intermediate bush-encroached rangeland, TH was positively correlated with LCD (r = 0.33), SCD (r = 0.36) and negatively correlated with GE (r = -0.93). LCD was positively correlated with SCD (r = 0.87), SCD (r = 0.43), while SCD was correlated with LBH (r = 0.38). Both TR and TSD were positively correlated with TE (r = 0.94-0.95). GSD was positively correlated with GE (r = 0.90).

In intensive bush-encroached rangeland, TH was positively correlated with LCD (r = 0.58), SCD (r = 0.32) and LBH (r = 0.52), respectively. LCD was positively correlated with SCD (r = 0.61), and LBH (r = 0.51), respectively. SCD was positively correlated with LBH (r = 0.48). TR was positively correlated with both TSD and TE (r = 0.94). TSD was positively correlated with TE (r = 0.89), while TE was correlated with GE (r = 0.84).
was the main contributor to the second axis (PC2). Exchangeable Ca, Mg, P and TSD were the main contributors to first axis (PC1). TR was the main contributor to the second axis (PC2). In intermediate bush-encroached
grassland, (PC1) explained 46% of the total data variation, and main contributors were exchangeable Mg, P, Ca, GE and GSD. PC2 which explained 21% of the data variation was related to TR. In intensive bush-encroached grassland, (PC1) which explained 47% of the data variation was related to total C, N opposed GE. PC2 was related to GSD, GR opposed to TH and P.

Figure 4.5: Principal component analysis of selected soil properties and vegetation components along different encroachment gradients in a savanna rangeland. Note: TH- tree height, LCD- longest crown diameter, SCD- shortest crown diameter, LBH- lowest browsable height, TR - tree richness, TSD - tree Shannon-wiener index, TE - tree evenness, BC - basal cover, GR - grass richness, GSD - grass Shannon wiener index, GE - grass evenness.
Table 4.3. Result of principal component analysis of vegetation parameters and soil nutrient loadings from open, intermediate and intensive shrub-encroached grassland.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Open PC1</th>
<th>PC2</th>
<th>Intermediate PC1</th>
<th>PC2</th>
<th>Intensive PC1</th>
<th>PC2</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>-0.76</td>
<td>0.37</td>
<td>-0.76</td>
<td>-0.52</td>
<td>0.87</td>
<td>-0.09</td>
</tr>
<tr>
<td>P</td>
<td>-0.64</td>
<td>0.4</td>
<td>-0.71</td>
<td>-0.51</td>
<td>0.86</td>
<td>-0.03</td>
</tr>
<tr>
<td>N</td>
<td>-0.81</td>
<td>0.01</td>
<td>-0.69</td>
<td>0.33</td>
<td>0.47</td>
<td>-0.85</td>
</tr>
<tr>
<td>K</td>
<td>-0.73</td>
<td>0.46</td>
<td>-0.63</td>
<td>-0.42</td>
<td>-0.92</td>
<td>0.19</td>
</tr>
<tr>
<td>Ca</td>
<td>-0.97</td>
<td>-0.03</td>
<td>-0.86</td>
<td>0.14</td>
<td>0.69</td>
<td>0.47</td>
</tr>
<tr>
<td>Mg</td>
<td>-0.73</td>
<td>0.22</td>
<td>-0.82</td>
<td>-0.06</td>
<td>0.53</td>
<td>0.79</td>
</tr>
<tr>
<td>TH</td>
<td>0.75</td>
<td>0.64</td>
<td>0.72</td>
<td>0.44</td>
<td>0.27</td>
<td>-0.84</td>
</tr>
<tr>
<td>LBH</td>
<td>0.69</td>
<td>-0.64</td>
<td>-0.2</td>
<td>0.21</td>
<td>-0.8</td>
<td>-0.4</td>
</tr>
<tr>
<td>TCA</td>
<td>0.69</td>
<td>0.43</td>
<td>0.36</td>
<td>0.08</td>
<td>0.79</td>
<td>0.5</td>
</tr>
<tr>
<td>TR</td>
<td>0.12</td>
<td>0.56</td>
<td>-0.47</td>
<td>0.84</td>
<td>-0.95</td>
<td>0.21</td>
</tr>
<tr>
<td>TSD</td>
<td>-0.93</td>
<td>0.23</td>
<td>-0.69</td>
<td>0.58</td>
<td>-0.94</td>
<td>0.27</td>
</tr>
<tr>
<td>TE</td>
<td>-0.84</td>
<td>0.39</td>
<td>-0.6</td>
<td>0.74</td>
<td>-0.82</td>
<td>0.3</td>
</tr>
<tr>
<td>BC</td>
<td>0.44</td>
<td>0.5</td>
<td>0.63</td>
<td>-0.56</td>
<td>-0.29</td>
<td>0.19</td>
</tr>
<tr>
<td>GR</td>
<td>-0.58</td>
<td>-0.8</td>
<td>0.82</td>
<td>0.54</td>
<td>0.18</td>
<td>0.8</td>
</tr>
<tr>
<td>GSD</td>
<td>-0.79</td>
<td>-0.41</td>
<td>-0.71</td>
<td>0.03</td>
<td>0.13</td>
<td>0.72</td>
</tr>
<tr>
<td>GE</td>
<td>-0.32</td>
<td>-0.5</td>
<td>-0.84</td>
<td>-0.15</td>
<td>-0.59</td>
<td>0.04</td>
</tr>
</tbody>
</table>
4.6. Discussion

4.6.1. Effect of shrub structure on grass species composition and diversity along encroachment gradient.

The tree stratum in the intensive bush-encroached grassland was dominated by *Vachellia hebeclada* (41%), *Dichrostachys cinerea* (39%), while the grass layer was dominated by *Panicum maximum* (90%). Our results concur with work of Kennard and Walker (1973) who found that *Panicum maximum* is a common understory grass species in encroached sites throughout southern Africa due to its higher survival in the shade than in the open. Trees facilitate understorey herbaceous growth and influence the overall species composition (Vetaas, 1992). The association between increasing tree canopy and *Panicum maximum* can be explained by enriched sub-canopy soil (Dye and Spear, 1982) and increased germination in the shade (Kennard and Walker, 1973). Trees and shrubs enrich the sub-canopy soil at the expense of the nutrient content of the open grassland, which may explain greater herbaceous production in intensively encroached grassland, an observation evident in our study and other studies elsewhere (Bernhard-Reversat, 1982; Belsky et al., 1989).

The increase in tree canopy cover and density mainly by *Vachellia* species and *Dichrostachys cinerea* along the encroachment gradient resulted in a 53% decline in grass species richness in the intensively bush encroached grassland. The decline in species richness due to encroachment, found at our study site is similar to the results obtained by Ratajczak et al. (2012) in a meta-analysis of 29 studies across 13 North American woody encroached grasslands and savannas that found a 45% decline in species richness. Our results are further supported by Price and Morgan (2008) who reported a 41% decline in species richness in Southern Australian woodlands under semi-arid environment. A recent study by Gobelle and Gure (2018) found that bush encroachment reduces species richness of herbaceous plants in Borana rangelands, Southern Ethiopia, while Thompson et al. (2017) found that species richness was lower inside shrub thickets in Virginia, USA. Recent work by Zhou et al. (2019) also found that shrub encroachment increases landscape heterogeneity by decreasing species richness in grasslands of northern China.

The decline in grass species richness along the encroachment gradient at our site can be attributed to the following reasons: The decrease in species richness can be linked to the increase in tree density and canopy cover from 800 trees ha$^{-1}$; 1.9 m$^2$ in open
grassland to 1700 trees ha\(^{-1}\); 3.1 m\(^2\) in the intensive shrub-encroached grassland. At our site, correlation analysis between woody plant components and herbaceous vegetation along encroachment gradient revealed that grass species richness, and grass species diversity were significantly negatively correlated (\(r = -0.97\)) with tree height (Table 4.2). A negative correlation between tree height and species richness has also been reported for other semi-arid savanna grasslands. Intensification of shrubs into open grasslands as consequence of encroachment moderates the microclimate and influences interception direct solar radiation (Belsky et al., 1989; Veetas, 1992). Along an encroachment gradient progressing from open alvar to intact dense scrub of *Juniperus communis* growing on shallow soils in Sweden, Bakker et al. (2014) found that shrub encroachment results in light attenuation between shrubs. Increasing tree density and canopy cover limits light penetration and availability (Légaré et al., 2001) leading to negative correlations of understory species richness with tree basal area (Hutchinson et al., 1999). An increase in tree canopy beyond a critical level results in the suppression of herbaceous plant diversity due to higher competitive effect of woody plants over grass species for light, soil water content and nutrients (Mckinney and Goodell, 2010). Savanna tree canopies have been shown to lower soil temperature and evapotranspiration, which subsequently enhances soil moisture content and influences herbaceous composition and diversity (Belsky et al., 1989; Veetas, 1992). Furthermore, greater accumulation of litter also contributes to alteration of the microclimate in shrub-encroached grasslands by reducing seed production and germination of herbaceous species (Brantley and Young, 2007; Price and Morgan, 2008; Bakker et al., 2014). Consequently, such changes lead to changes in understorey herbaceous vegetation.

Not only does woody plant encroachment affect species richness and diversity but alters the structure of grasslands through a reduction in vegetation cover (Turnbull et al., 2010). At our site, basal cover minimally declined along the encroachment gradient from 18.8% in open to 17.2% in intensive shrub-encroached grassland (Figure 4.3). A study by Turnbull et al. (2010) that determined the spatial structure of biotic and abiotic factors along a shrub-encroachment gradient in central New Mexico, USA under a semi-arid climate also found a decrease in vegetation cover from 45.5% to 23.3%, which was accompanied by a concurrent decline in the area covered by grasses. According to Wright et al. (2013), the rapid loss of herbaceous vegetation results in an increase in canopy cover of woody vegetation, an observation evident along the
encroachment gradient at our site. Increases in canopy cover and density of woody plants above threshold levels have been shown to influence runoff and erosion processes, in turn, directly affecting the redistribution of nutrients in shrub-encroached grasslands (Turnbull et al., 2010).

4.6.2. Relationship between vegetation parameters and soil nutrients along encroachment gradient

Macro-nutrients (total N and P) and exchangeable base cations (Ca and Mg) in the topsoil layer (0-10 cm) increased with increasing tree density and cover along the encroachment gradient, except K, which declined (Appendix 2). Similar to our results, Aweto and Dikinya (2003) found an increase in exchangeable P, calcium (Ca), Mg and cation exchange capacity (CEC) between tree canopies in the topsoil layer (0-10 cm) of a semi-arid savanna rangeland in Botswana.

Total C content increased along the encroachment gradient at our site. González-Roglich et al. (2014) also found an increase in soil C along a woody plant gradient in Argentina. There are a number of possible factors and mechanisms increasing C and nutrients soil along the bush encroachment gradient. Holdo and Mack (2014) suggested that the variation in tree canopy cover is the biotic driver of C and nutrient dynamics in the top 10 cm of savanna soils in Kruger National Park, South Africa. Indeed, increases in woody plant cover alters C and nutrient cycling. Litter inputs shift from herbaceous to tree-derived, which affects the litter quality and quantity, and in turn alter soil C and nutrient dynamics (Nunes Biral et al., 2019). The mechanisms driving C accumulation following shrub encroachment into previously open grasslands may be associated with: (i) higher rates of net primary productivity in bush-encroached compared to open grasslands. With bush encroachment of grasslands, there is an increase in plant-bound C due to increasing woodiness of the vegetation (Weintraub and Schimel, 2005); (ii) increased biochemical recalcitrance of litter inputs in shrub-encroached grassland; and (iii) physical protection of organic matter inputs within soil structure (González-Roglich et al., 2014).

Trees maintain soil fertility in semi-arid savannas (Bernhard-Reversat, 1982). The tree species influence the size and distribution of nutrient pools in soil (Binkley, 1994). Previous studies by Belsky et al. (1989) and Liu et al. (2011) reported that a shift from open to bush-encroached grasslands leads to the accumulation of soil organic matter added as litter and debris to the soil surface. A recent study by Dlamini et al. (2019) at
our site found that organic matter is a decisive agent conditioning nutrient pools in the loamy sand soil through the release of nutrients from organic debris and litter via decomposition processes driven by biological activity. This accumulation of soil organic matter under shrublands provide an important nutrient pool that provides shrubs with a competitive advantage over herbaceous plants, especially during times of nutrient limitation (Turnbull et al., 2010).

4.7. Conclusion

In this study, the main objectives were to determine the effect of increasing tree density and cover on grass species richness, diversity, evenness and soil nutrients along a shrub encroachment gradient. The increase in tree canopy density and cover along an encroachment gradient dominated by Vachellia species and Dichrostachys cinerea at our site led to a substantial decline in grass species richness in the intensive bush encroached grassland. This was accompanied by a decrease in basal cover, often associated with degradation. This may profound implications for future management of the savanna rangeland. Transition from open to intensive shrub-encroached grasslands led to an increase in surface nutrients in the shallow plinthic soil. A greater understanding of the mechanisms underlying interactions between shrubs and grasses may provide strategies for management of semi-arid savannas in shallow soils limited by depth for root penetration and water availability.
REFERENCES


organic carbon in complex landscapes: an example of grassland undergoing
Maestre, F.T., Bowker, M.A., Puche, M.D., Belén Hinojosa, M., Martinez, I., Garcia-
Palacios, P., Castillo, A.P., Soliveres, S., Luzuriaga, A.L. and Sánchez, A.M.
2009. Shrub encroachment can reverse desertification in semi-arid
McKinney, A.M. and Goodell, K. 2010. Shading by invasive shrub reduces seed
production and pollinator services in a native herb. Biological Invasions
12:2751-2763.
Moleele, N.M. and Perkins, J.S. 1998. Encroaching woody plant species and
boreholes: is cattle density the main driving factor in the Olifants Drift communal
grazing lands, south-eastern Botswana? Journal of Arid Environments 40:245-
253.
Perspective: Learning new tricks from old trees: revisiting the savanna
Mucina, L. and Rutherford, M.C. 2006. The Vegetation of South Africa, Lesotho and
Swaziland. South African National Biodiversity Institute.
Muenchh. And Juniperus virginiana L. in the Tallgrass Prairie of Oklahoma, USA
Doi:10.3390/f10040329.
richness of herb-rich woodlands in southern Australia. Ecological Society of
Australia 33:278-289.
diversity across North American grasslands and savannas. Ecology 93:697-
703.


CHAPTER 5
SUMMARY AND CONCLUSION

The increase in woody species has been an on-going problem in semi-arid rangelands. Bush encroachment remains a threat to pastoralists and farm managers. The proliferation of woody species in savanna rangelands alters the vegetation structure, creating enclosures and limiting movement of grazing livestock. The main aim of this study was to investigate the impact of bush encroachment on herbaceous vegetation and selected soil properties in a savanna rangeland. Accordingly in chapter 3, a study was conducted to assess woody species composition and structure along an encroachment gradient and to explore the relationship between woody and herbaceous vegetation. It was shown in this study that tree density and cover increased along the bush encroachment gradient, and was dominated by leguminous Vachellia spp. and Dichrostachys cinerea. Increasing woody density and cover especially in the intensive bush encroached rangeland resulted in an increase in the shade tolerant decreaser species P. maximum.

Chapter 4 revealed the effect of increasing tree density on grass species richness, diversity, evenness and soil nutrients along the bush encroached rangeland. An increase in woody species resulted in a significant decline in grass species richness. The decline in grass richness was mainly associated with increasing tree density and cover across the bush encroached gradient. The decline in grass richness at the site may over time lead to a decline in basal cover, which may promote degradation of the rangeland. The results also revealed that woody plants alter the macro-nutrients of the soil specifically increasing carbon, nitrogen, phosphorus calcium and magnesium.

The study also uncovered some areas of research which could be addressed in the future. There is a need to accurately quantify the tree architecture of savanna rangelands in order to better understand their interactions with herbaceous vegetation. A much greater effort could be made in determining how soil nutrients and seedbank diversity respond to dynamic vegetation cover alterations associated with bush encroachment especially in shallow soils limited by depth.
APPENDICES

Appendix 1: One-way analysis of variance for grasses and trees in open, intermediate and intensive bush encroached savanna grassland.

### Basal cover

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between groups</td>
<td>3</td>
<td>84.744</td>
<td>28.248</td>
<td>0.904</td>
<td>0.448</td>
</tr>
<tr>
<td>Within groups</td>
<td>41</td>
<td>1281.841</td>
<td>31.264</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>44</td>
<td>1366.585</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Grass species richness

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between groups</td>
<td>2</td>
<td>4.143</td>
<td>2.071</td>
<td>19.02</td>
<td>0</td>
</tr>
<tr>
<td>Within groups</td>
<td>15</td>
<td>1.633</td>
<td>0.109</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>17</td>
<td>5.776</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Grass species diversity

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between groups</td>
<td>2</td>
<td>1.109</td>
<td>0.555</td>
<td>8.093</td>
<td>0.004</td>
</tr>
<tr>
<td>Within groups</td>
<td>15</td>
<td>1.028</td>
<td>0.069</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>17</td>
<td>2.137</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Grass species evenness

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between groups</td>
<td>2</td>
<td>0.44</td>
<td>0.022</td>
<td>0.894</td>
<td>0.43</td>
</tr>
<tr>
<td>Within groups</td>
<td>15</td>
<td>0.373</td>
<td>0.025</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>17</td>
<td>0.418</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Tree species richness

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between groups</td>
<td>2</td>
<td>0.775</td>
<td>0.387</td>
<td>4.093</td>
<td>0.038</td>
</tr>
<tr>
<td>Within groups</td>
<td>15</td>
<td>1.42</td>
<td>0.095</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>17</td>
<td>2.195</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Tree species diversity

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between groups</td>
<td>2</td>
<td>1.015</td>
<td>0.508</td>
<td>4.353</td>
<td>0.032</td>
</tr>
<tr>
<td>Within groups</td>
<td>15</td>
<td>1.75</td>
<td>0.117</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>17</td>
<td>2.765</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Tree species evenness

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between groups</td>
<td>2</td>
<td>0.275</td>
<td>0.137</td>
<td>4.986</td>
<td>0.022</td>
</tr>
<tr>
<td>Within groups</td>
<td>15</td>
<td>0.414</td>
<td>0.028</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>17</td>
<td>0.689</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Tree Height

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Sum of Squares</th>
<th>Mean Square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between Groups</td>
<td>2</td>
<td>137.136</td>
<td>68.568</td>
<td>25.71</td>
<td>0</td>
</tr>
<tr>
<td>Within Groups</td>
<td>159</td>
<td>424.06</td>
<td>2.667</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>df</td>
<td>Sum of Squares</td>
<td>Mean Square</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>----------------</td>
<td>----</td>
<td>----------------</td>
<td>-------------</td>
<td>-------</td>
<td>------</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>161</td>
<td>561.197</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Longest Crown Diameter</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between Groups</td>
<td>2</td>
<td>17.625</td>
<td>8.813</td>
<td>6.641</td>
<td>0.002</td>
</tr>
<tr>
<td>Within Groups</td>
<td>159</td>
<td>211.001</td>
<td>1.327</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>161</td>
<td>228.627</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Shortest Crown Diameter</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between Groups</td>
<td>2</td>
<td>15.332</td>
<td>7.666</td>
<td>6.161</td>
<td>0.003</td>
</tr>
<tr>
<td>Within Groups</td>
<td>159</td>
<td>197.821</td>
<td>1.244</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>161</td>
<td>213.152</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Lowest Browsable Height</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between Groups</td>
<td>2</td>
<td>16.528</td>
<td>8.264</td>
<td>7.2</td>
<td>0.001</td>
</tr>
<tr>
<td>Within Groups</td>
<td>159</td>
<td>182.503</td>
<td>1.148</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>161</td>
<td>199.031</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Appendix 2: One-way analysis of variance for soil properties in open, intermediate and intensive bush encroached savanna grassland.

<table>
<thead>
<tr>
<th></th>
<th>Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Total C</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between Groups</td>
<td>1246.482</td>
<td>2</td>
<td>623.241</td>
<td>34.774</td>
<td>.000</td>
</tr>
<tr>
<td>Within Groups</td>
<td>1863.961</td>
<td>104</td>
<td>17.923</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>3110.443</td>
<td>106</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Total N</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between Groups</td>
<td>6.558</td>
<td>2</td>
<td>3.279</td>
<td>17.600</td>
<td>.000</td>
</tr>
<tr>
<td>Within Groups</td>
<td>18.818</td>
<td>104</td>
<td>.186</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>25.376</td>
<td>103</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Soil P</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between Groups</td>
<td>244.380</td>
<td>2</td>
<td>122.190</td>
<td>26.126</td>
<td>.000</td>
</tr>
<tr>
<td>Within Groups</td>
<td>486.405</td>
<td>104</td>
<td>4.677</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>730.785</td>
<td>106</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Soil Mg</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between Groups</td>
<td>17917.454</td>
<td>2</td>
<td>8958.727</td>
<td>12.433</td>
<td>.000</td>
</tr>
<tr>
<td>Within Groups</td>
<td>74935.294</td>
<td>104</td>
<td>720.532</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>92852.748</td>
<td>106</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Soil K</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between Groups</td>
<td>84809.433</td>
<td>2</td>
<td>42404.717</td>
<td>4.011</td>
<td>.021</td>
</tr>
<tr>
<td>Within Groups</td>
<td>1099570.753</td>
<td>104</td>
<td>10572.796</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1184380.187</td>
<td>106</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Soil Ca</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between Groups</td>
<td>1535285.129</td>
<td>2</td>
<td>767642.564</td>
<td>26.781</td>
<td>.000</td>
</tr>
<tr>
<td>Within Groups</td>
<td>2981035.918</td>
<td>104</td>
<td>28663.807</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>4516321.047</td>
<td>106</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>