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

List of figures

List of tables

List of appendices

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 (CO_2), result in the increase of C_3 woody species at the expense of C_4 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 a 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

Asner, G. P., Elmore, A. J., Olander, L. P., Martin, R. E. and Harris. A. T. 2004. Grazing systems, ecosystem responses and global change. *Annual Review Environmental Resources* 29:261-299.

Belayneh, A. and Tessema, Z. K. 2017. Mechanisms of bush encroachment and its inter-connection with rangeland degradation in semi-arid African ecosystems: a review. *Journal of Arid Land* 9:299-312.

Devine, A.P., McDonald, R.A., Quaife, T. and Maclean, I.M.D. 2017. Determinants of woody encroachment and cover in African savannas. *Oecologia* 183:939-951.

Eldridge, D.J. and Solivers, S. 2015. Are shrubs really a sign of declining ecosystem function? Disentangling the myths and truths of woody encroachment in Australia. *Australian Journal of Botany* 62:594-608.

Fynn, R. W. S. and O'connor, T. G. 2000. Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savannah, South Africa. *Journal of Applied ecology* 37:491-507.

Guido, A., Salengue., E. and Dresseno, A. 2017. Effect of shrub encroachment on vegetation communities in Brazilian forest-grassland mosaics. *Perspectives in ecology and conservation* 15:52-55.

Kassahun, A., Snyman, H.A. and Smit, G.N. 2008. Impact of rangeland degradation on the pastoral production systems, livelihoods and perceptions of the Somali pastoralists in Eastern Ethiopia. *Journal of Arid Environments* 72:1265-1281.

Kraaij, T. and Ward, D. 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant ecology* 186:235-246.

Li, H., Shen, H., Chen, L., Liu, T., Hu, H., Zhao, X., Zhou, L., Zhang, P. and Fang, J. 2016. Effects of shrub encroachment on soil organic carbon in global grasslands. *Scientific reports* 6:28974.

Liu, F., Wu, X. B., Bai, E., Boutton, T. W. and Archer, S.R. 2011. Quantifying soil organic carbon in complex landscapes: an example of grassland undergoing encroachment of woody plants. *Global Change Biology* 17:1119-1129.

Maestre, F. T., Eldridge, D. J. and Soliveres, S. 2016. A multifaceted view on the impacts of shrub encroachment. *Applied Vegetation Science* 19:369-370.

Maestre, F.T., Bowker, M.A., Puche, M.D., Hinojosa, M.B., Martinez, I., Garcia-Palacios, P., Castillo, A.P., Soliveres, S., Luzuriaga, A.L., Sanchez, A.M., Carreira, J.A., Gallardo, A. and Escudero, A. 2009. Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. *Ecology letter* 12:930-941.

Maitima, J.M., Mugatha, S.M., Reid, R.S., Gachimbi, L.N, Majule, A., Lyaruu, H., Pomery, D., Mathai, S and Mugisha, S. 2009. The linkages between land use change, land degradation and biodiversity across East Africa. African Journal of Environmental Science and Technology 3:310-325

Mureva, A. and Ward, D. 2016. Spatial patterns of encroaching shrub species under different grazing regimes in a semi-arid savanna, eastern karoo, South Africa. *African Journal of Range and Forage Science* 33:77-80.

Mussa, M., Hashim, H. and Teha, M. 2016. Rangeland Degradation: Extent, Impacts, and Alternative Restoration Techniques in the Rangelands of Ethiopia. Tropical and Subtropical Agroecosystems 19:305-318.

Price, J.N. and Morgan, J.W. 2008. Woody plant encroachment reduces species richness of herb-rich woodlands in southern Australia. *Ecological Society of Australia* 33:278-289.

Ravi, S., Breshears, D.D., Huxman, T.E. and D’Odorico, P. 2010. Land degradation in drylands: Interactions among hydrologic- aeolian erosion and vegetation dynamics. *Geomorphology* 116:236-245.

Ringrose, S., Chipanshi, A. C., Chanda, A. C., Matheson, R., Motoma, L., Magole, I., Jellema, A., 2002. Climate-and human-induced woody vegetation changes in Botswana and their implications for human adaptation. *Environmental Management* 30:98-109.

Roques, K.G., O’connor, T.G. and Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of applied ecology* 38:268-280.

Smit, G. N. 2004. An approach to tree thinning to structure southern African savannas for long-term restoration from bush encroachment. *Journal of Environmental Management* 71:179-191.

Smit, G. N. and Rethman, N. F. G. 1999. The influence of tree thinning on the establishment of herbaceous plants in a semi-arid savanna of Southern Africa. *African Journal of Range and Forage Science* 16:9-18.

Ward, D. 2005. Do we understand the causes of bush encroachment in African savannas? *African Journal of Range & Forage Science* 22:101-105.

CHAPTER 2

LITERATURE REVIEW

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.

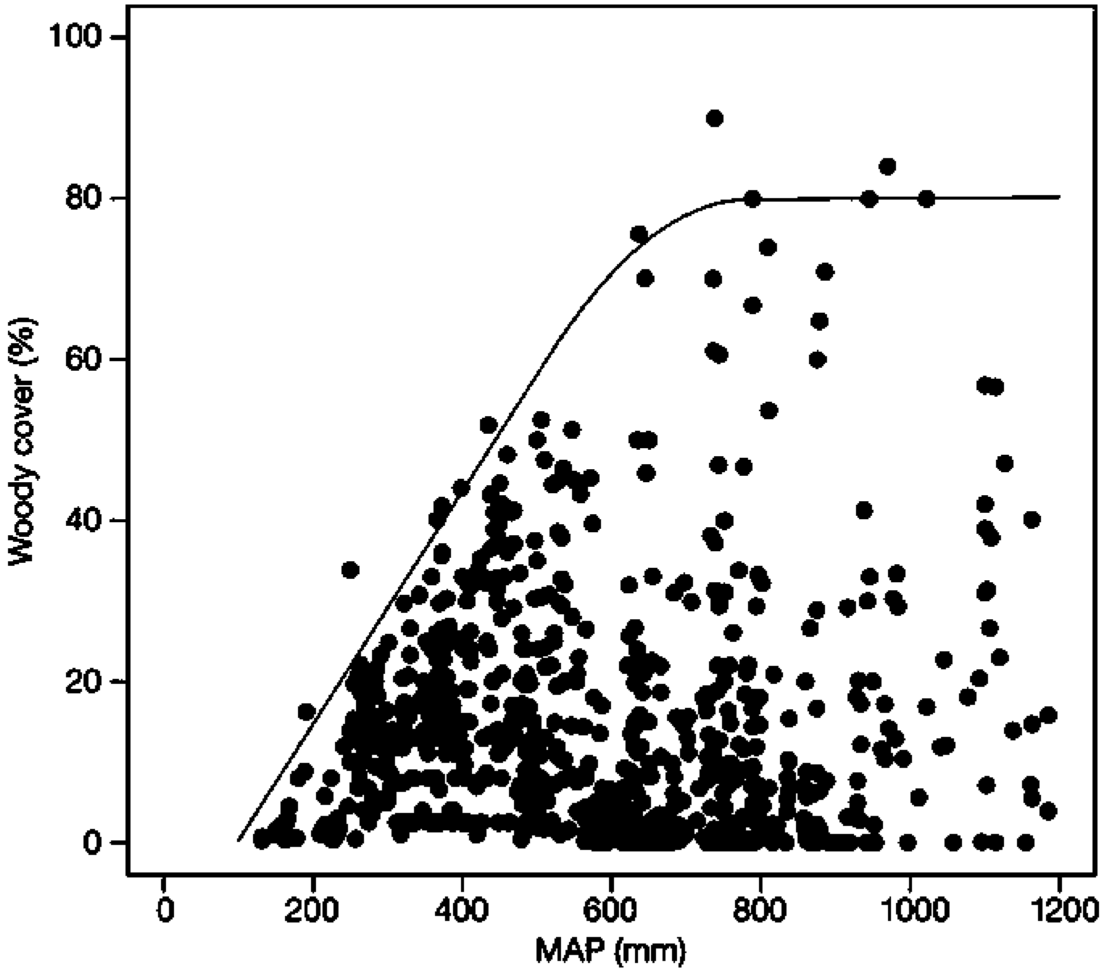

Figure 2.1 Relationship between woody cover and mean annual precipitation in Africa (Sankaran *et al.*, 2005).

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 (CO_2)

Atmospheric CO_2 concentration facilitates the growth and functioning of plants, which is known to increase woody plant cover. Industrialization has increased atmospheric CO_2 from 277 ppm to 397 ppm in 2013 (O'connor *et al*., 2014). According to Archer *et al*. (2017), increased CO_2 concentrations restrict photosynthesis by C_{34}grasses and this favours C_3 woody plants. An increase in CO_2 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 CO_2 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

(Bilotta *et al*., 2007; Tessema *et al*., 2011). 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

Adams, M.E. 1967. A study of the ecology of *Acacia mellifera*, *A. seyal* and *Balanites aegyptica* in relation to land-clearing. *Journal of Applied Ecology* 4: 221-237.

Archer, S. R., Andersen, E. M., Predick, K. I., Schwinning, S., Steidl, R. J. and Woods, S. R. 2017. Woody Plant Encroachment: Causes and Consequences. *Rangeland Systems, Springer Series on Environmental Management* DOI 10.1007/978-3-319-46709-2_2.

Báez, S. and Collins, S. L. 2008. Shrub Invasion Decreases Diversity and Alters Community Stability in Northern Chihuahuan Desert Plant Communities. *PLoS ONE* 3:2332.

Belsky, A.J. 1994. Influences of trees on savanna productivity: Tests of shade, nutrients and tree-grass competition. *Ecology* 75:922-932.

Bilotta, G.S., Brazier, R.E. and Haygarth, P.M. 2007. The impacts of grazing animals on the quality of soils, vegetation and surface waters in intensively managed grasslands. *Advances in Agronomy* 94:238-279.

Bond, W.J. 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* 9:973-982.

Britz, M.L. and Ward, D. 2007. Dynamics of woody vegetation in a semi-arid savanna, with a focus on bush encroachment. *African Journal of Range & Forage Science* 24:131-140.

Chen, L., Li, H., Zhang, P., Zhao, X., Zhou, L., Liu, T., Hu, H., Bai., Y., Shen, H. and Fang, J. 2015. Climate and native grassland vegetation as drivers of the community structures of shrub-encroached grasslands in Inner Mongolia, China. Landscape ecology 30:1627-13641.

DeMarco, J., Filley, T. and Throop, H.L. 2016. Patterns of woody plant-derived soil carbon losses and persistence after brush management in a semi-arid grassland. *Plant Soil* 406:277-293.

Devine, A.P., McDonald, R.A., Quaife, T. and Maclean, I.M.D. 2017. Determinants of woody encroachment and cover in African savannas. *Oecologia* 183:939-951.

Doetterl, S., Berhe, A.S., Nadeu, E., Wang, Z., Sommer, M. and Fiener, P. 2016. Erosion, deposition, and soil carbon: A review of process-level controls, experimental tools and models to address C cycling in dynamic landscapes. *Earth-Science Reviews* 154:102-122.

Eldridge, D.J., Bowkerb, M.A., Maestre, F.T., Roger, E., Reynolds, J.F. and Whitforde, W.G. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters* 14:709-722.

Grygoruk, M., Batelaan, O., Mirosław-Świątek, D, Szatyłowicz, J. and Okruszko, T. 2014. Evapotranspiration of bush encroachments on a temperate mire meadow – A nonlinear function of landscape composition and groundwater flow. *Ecological Engineering* 73:598-609.

Guido, A., Salengue., E. and Dresseno, A. 2017. Effect of shrub encroachment on vegetation communities in Brazilian forest-grassland mosaics. *Perspectives in ecology and conservation* 15:52-55.

Groengroeft, A., de Blécourt, M., Classen, N., Landschreiber, L. & Eschenbach, A. 2018. Acacia trees modify soil water dynamics and the potential groundwater recharge in savanna ecosystems. Klaus Hess Publishers, Göttingen andWindhoek. 177 - 186.

Higgins, S. I., Bond, W. J. and Trollope, W. S. W. 2000. Fire resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88:213-229.

Keno, B. and Suryabhagavan, K.V. 2014. Multi-Temporal Remote Sensing of Landscape Dynamics and Pattern Changes in Dire District, Southern, Ethiopia. *Journal of Earth Science and Climate Change* 5:226-231.

Lesoli, M.S., Gxasheka, M., Solomon, T.B. and Moyo, B. 2013. Integrated Plant Invasion and Bush Encroachment Management on Southern African Rangelands. Herbicides: Current Research and Case Studies in Use. INTECH 259-313.

Li, P.X., Wang, N., He, W.M., Krüsi, B.O., Gao, S.Q., Zhang, S.M., Yu, F.H., Dong, M. 2008. Fertile islands under Artemisia ordosica in inland dunes of northern China: Effects of habitats and plant developmental stages. *Journal of Arid Environments* 72:953-963.

Liu, F., Wu, X. B., Bai, E., Boutton, T. W. and Archer, S.R. 2011. Quantifying soil organic carbon in complex landscapes: an example of grassland undergoing encroachment of woody plants. *Global Change Biology* 17:1119-1129.

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.

Moleele, N.M., Ringrose, S., Matheson, W. and Vanderpost, C. 2011. More woody plants? The status of bush encroachment in Botswana's grazing area. *Journal of Environmental Management* 64:3-11.

Moustakas, A., Wiegand, K., Meyer, K.M., Ward, D and Sankaran., M. 2010. Learning new tricks from old trees: revisiting the savanna question. *Frontiers of Biogeography* 2:47-53.

Mureva, A. and Ward, D. 2016. Spatial patterns of encroaching shrub species under different grazing regimes in a semi-arid savanna, eastern karoo, South Africa. *African Journal of Range and Forage Science* 33:77-80.

O'Connor, T. G., Puttick, J. R. and Hoffman, M. T. 2014. Bush encroachment in southern Africa: changes and causes. *African Journal of Range and Forage Science* 31:67-88.

Reed, M.S., Stringer, L.C., Doughill, A.J., Perkins, J.S., Atlhopheng, J.R., Mulale, K. and Favretto, N. 2015. Reorienting land degradation towards sustainable land management: Linking sustainable livelihoods with ecosystem service in rangeland systems. *Journal of Environmental Management* 151:472-485.

Ridolfi, L., Laio, F. and D'Odorico, P. 2008. Fertility island formation and evolution in dryland ecosystems. *Ecology and Society* 13(1): 5.

Riginos. C. 2009. Grass competition suppresses savanna tree growth across multiple demographic stages. *Ecology* 90:335-340.

Roques, K.G., O'connor,T.G. and Watkinson, A.R. 2016. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* 38:268-280.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, A.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral., C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L. Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. and Zambatis, N. 2005. Determinants of woody cover in African savannas. *Nature* 43 doi:10.1038/nature04070

Scholes, R.J. and Archer, S.R. (1997) Tree-grass interactions in savannas. *Annual Review of Ecology, Evolution, and Systematics* 28:517:544.

Smit, G.N. 2004. An approach to tree thinning to structure southern African savannas for long-term restoration from bush encroachment. *Journal of Environmental Management* 71:179-191.

Tessema, Z.K., de Boer, W.F., Baars, R.M.T. and Prins, H.H.T. 2011. Changes in soil nutrients, vegetation structure and herbaceous biomass in response to grazing in semi-arid savanna of Ethiopia. *Journal of Arid Environments* 75:662-670.

Tews, J., Blaum, N. and Jeltsch, F. 2004. Structural and Animal Diversity in Arid and Semi-Arid Savannas of the Southern Kalahari. *Annals of Arid Zone* 43:413-425.

Throop, H. and Archer, S.R. 2008. Shrub (*Prosopis velutina*) encroachment in a semi-desert grassland: spatial–temporal changes in soil organic carbon and nitrogen pools. *Global Change Biology* 14:2420-2431.

Trollope, W.S.W. 1974. Role of fire in preventing bush encroachment in the Eastern Cape. *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa* 9:67-72.

van Auken, O. W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management* 90:2931-2942.

Wang, L. D’Odorico, P., Evans, J. P., Eldridge, D. J., McCabe, M. F., Caylor, K. K. and King, E. G. 2012. Dryland ecohydrology and climate change: critical issues and technical advances. *Hydrology and Earth System Science* 16:2585–2603.

Ward, D. 2005. Do we understand the causes of bush encroachment in African savannas? *African Journal of Range & Forage Science* 22:101-105.

Wiegand, K., Saltz, D. and Ward, D. 2006. A patch-dynamics approach to savanna dynamics and woody plant encroachment - Insights from an arid savanna. *Perspectives in Plant Ecology, Evolution and Systematics* 7:229-242.

Wiegand, K., Ward, D. and Saltz, D. 2005. Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer*. Journal of Vegetation Science* 16: 311-320.

Wright, A., Schnitzer, S. A., Dickie, I. A., Gunderson, A. R., Pinter, G. A., Mangan, S. A. and Reich, P. B. 2013. Complex facilitation and competition in a temperate grassland: loss of plant diversity and elevated CO_2 have divergent and opposite effects on oak establishment. *Oecologia* 171:449-458.

Yusuf, H.M., Treydte, A.C. and Sauerborn, J. 2015. Managing Semi-Arid Rangelands for Carbon Storage: Grazing and Woody Encroachment Effects on Soil Carbon and Nitrogen. *PLoS ONE* 10:e0109063.

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 m^2) (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.

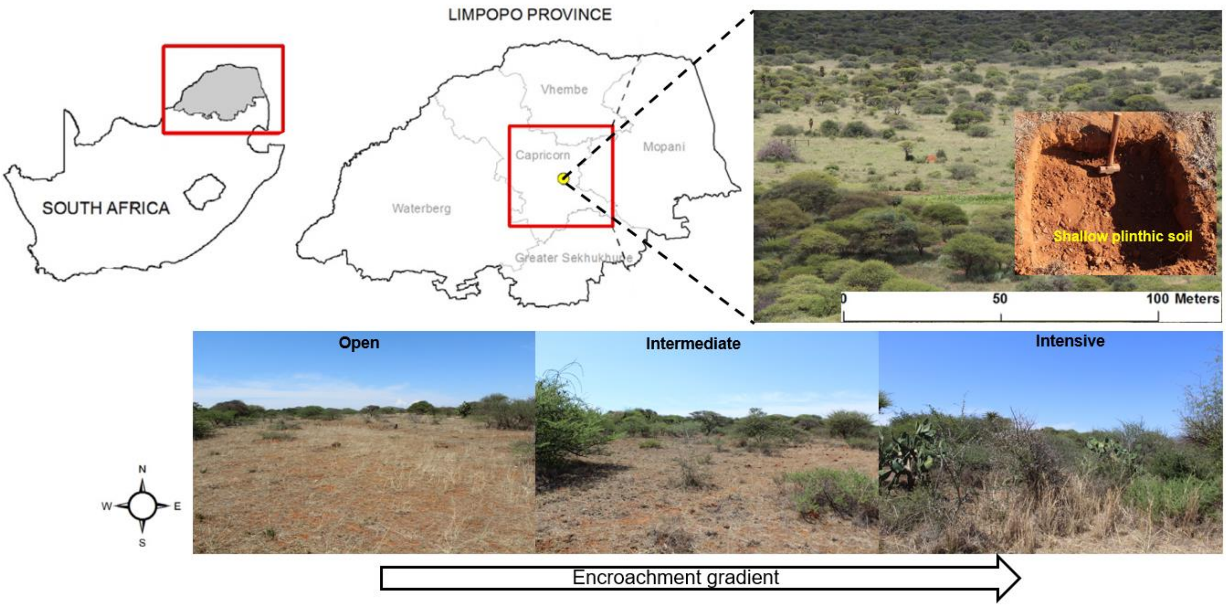

Figure 3.1. Location of the study site and photographs showing encroachment gradient spanning from open, intermediate and intensive along the savanna rangeland as well soil profile of the shallow plinthic soil.

Table 3.1. Woody and herbaceous plant species mean tree density, slope gradient and soil type for three encroached intensities (open, intermediate and intensive).

Intensity	**TD**	**Location**	**Elevation**	**Slope**	**Soil**	**Species**
	Trees. ha^{-1}		**(m)**	**(%)**		
Open	800	S23º50,659' E29º41,974'	1236-1238	0-2	Westleigh	Trees: *Vachellia hebeclada, Vachellia karoo, Dichrostachys cinerea, Opuntia ficus indica, Ziziphus mucronata.* Grasses: *Aristida congesta, Brachiaria nigropedata, Cynodon dactylon, Digiteria eriantha, Eragrostis rigidior, Eragrostis superba, Heteropogon contortus, Panicum natalense, Schmidtia pappophoroides, Themeda triandra.*
Intermediate	1300	S23º50,704' E29º42,008'	1239-1240	0-1	Westleigh	Trees: Vachellia *hebeclada,* Vachellia *karoo,* Vachellia *tortillis, Aloe ferox, Dichrostachys cinerea, mimusops caffra, Opuntia ficus indica.* Grasses: *Aristida congesta, Brachiaria nigropedata, Cynodon dactylon, Digiteria eriantha, Eragrostis lehmanniana, Eragrostis rigidior, Eragrostis superba, Heteropogon contortus, Melinis repens, Panicum maximum, Panicum natalense, Pogonarthria squarossa, Schmiditia pappophoroides, Themeda triandra.*
Intensive	1700	S23º50,673' E29º41,948'	1234	0-1	Westleigh	Trees: *Vachellia hebeclada, Vachellia karoo, Aloe ferox, Dichrostachys cinerea.* Grasses: *Cynodon dactylon, Eragrostis lehmanniana, Eragrostis rigidior, Heteropogon contortus, Panicum maximum.*

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).

$$TCA = (\frac{d1 \times d2 \ \times \pi}{4})$$

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:

$$H = -\sum_{i=1}^{s}(Pi \ \ ln\, Pi)$$

Where *H* is the Shannon-Wiener index (the measure of species diversity), Pi 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.

			Encroachment intensity		
Species	**Palatability**	**Presence of Thorns**	**Open**	**Intermediate**	**Intensive**
			Relative abundance (%)		
Vachellia *hebeclada*	+	+	36	13	41
Vachellia *Karoo*	+	+	33	4	18
Vachellia *tortillis*	+	+	-	24	-
Aloe ferox	+	+	-	32	2
Dichrostachys cinerea	+	+	3.6	2	39
Mimusops caffra	+	-	-	4	-
Opuntia ficus indica	+	+	24	21	-
Ziziphus mucronata	+	+	3.4	-	-

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).

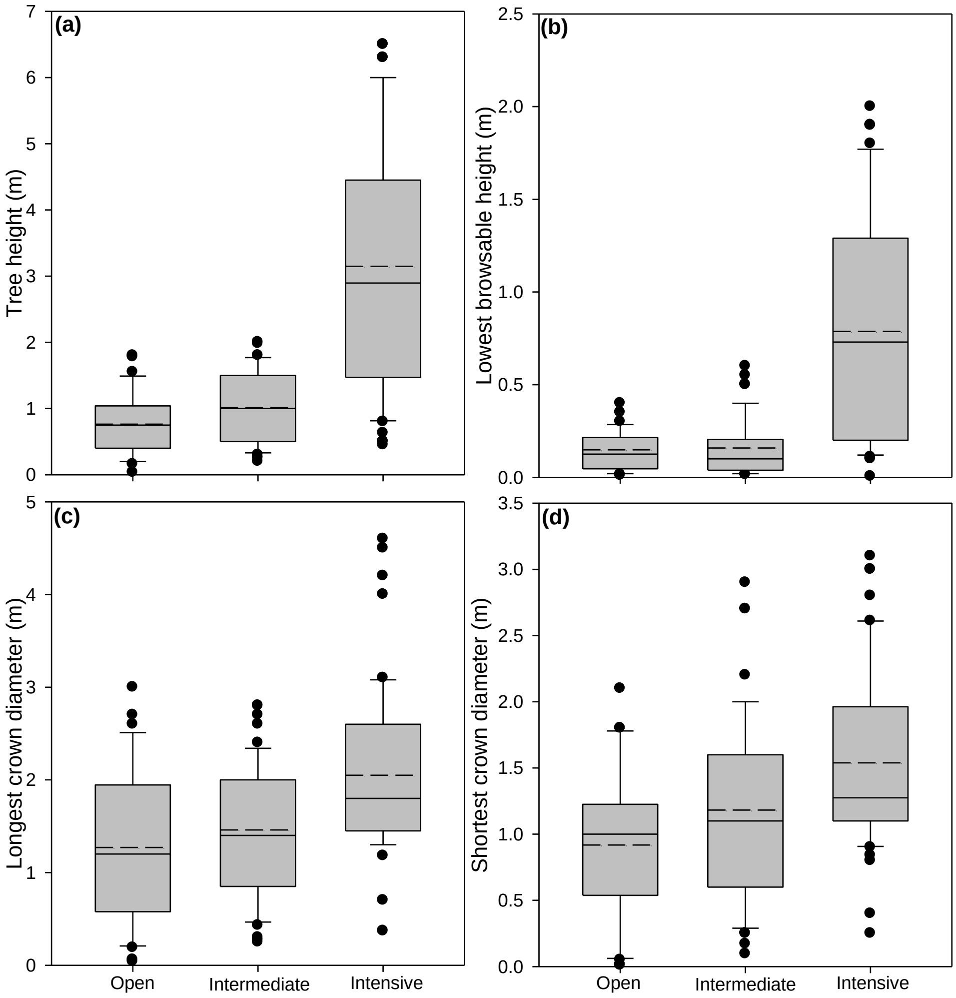

Figure 3.2. Distribution of (a) tree height (b) lowest browsable height (c) longest crown diameter and (d) shortest crown diameter in open, intermediate and intensive bush-encroached rangeland. Graphic is based on six plots per encroachment level, box plots, with whiskers extending from the 25th and 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).

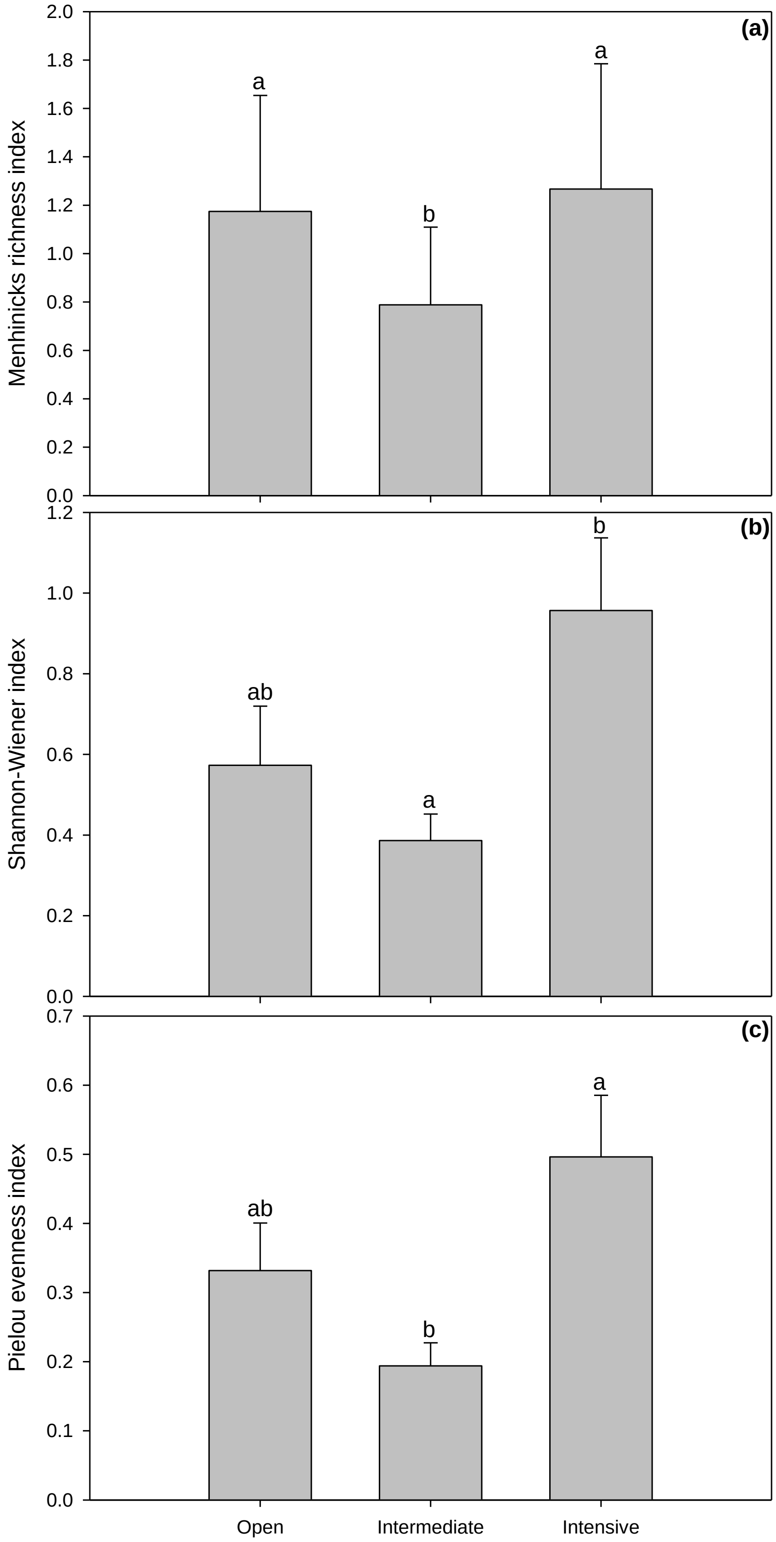

Figure 3.3. Comparison of tree richness (a), Shannon-Wiener diversity (b) and Pielou’s evenness (c) indexes in open, intermediate and intensive bush encroached rangeland. The value is the mean ± standard error obtained from six plots in each encroachment level. Different superscripts above the bars indicate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

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

Angassa, A. and Oba, G. 2010. Effects of grazing pressure, age of enclosures and seasonality on bush cover dynamics and vegetation composition in southern Ethiopia. *Journal of arid environments* 74:111-120.

Archer, S. R., Andersen, E. M., Predick, K. I., Schwinning, S., Steidl, R. J. and Woods, S. R. 2017. Woody Plant Encroachment: Causes and Consequences. *Rangeland Systems, Springer Series on Environmental Management* DOI 10.1007/978-3-319-46709-2_2.

Belay, T. and Moe, S.R. 2015. Assessing the Effects of Woody Plant Traits on Understory Herbaceous Cover in a Semiarid Rangeland. *Journal of Environmental management* 56:165-75.

Belayneh, A. and Tessema, Z. K. 2017. Mechanisms of bush encroachment and its inter-connection with rangeland degradation in semi-arid African ecosystems: a review. *Journal of Arid Land* 9:299-312.

Bond, W.J. 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* 9:973-982.

Breebaart, L., Bhikraj, R. and O’Connor, TG. 2002. Dietary overlap between Boer goats and indigenous browsers in a South African savanna. *African Journal of Range & Forage Science* 19: 13– 20

Danckwerts, J.E. and Stuart-Hill,G.C. 1987. Adaptation of a decreaser and an increaser grass species to defoliation in semi-arid grassveld. *Journal of the grassland society of Southern Africa* 2:68-73.

Devine, A.P., McDonald, R.A., Quaife, T. and Maclean, I.M.D. 2017. Determinants of woody encroachment and cover in African savannas. *Oecologia* DOI 10.1007/s00442-017-3807-6.

du Plessis, I., van der Waal, C. and Webb, E.C. 20014. A comparison of plant form and browsing height selection of four small stock Breeds-Preliminary results. *South African Journal of Animal Science* 34:31-34.

Eldridge, D.J., Bowkerb, M.A., Maestre, F.T., Roger, E., Reynolds, J.F. and Whitforde, W.G. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters* 14:709-722.

Gobelle, S.K. and Gure, A. 2018. Effects of bush encroachment on plant composition, diversity and carbon stock in Borana rangelands, Southern Ethiopia. *International Journal of Biodiversity and Conservation* 10:230-245.

Götmark, F., Götmark, E. and Jensen, A.M. 2016. Why Be a Shrub? A Basic Model and Hypotheses for the Adaptive Values of a Common Growth Form. Frontiers in Plant Science 7: 1095.

Gxasheka, M. 2013. *Euryops floribundus* encroachment in Eastern Cape communal rangelands: Indigenous and scientific understanding of effects on range ecology, and food Security. MSc Dissertation. University of Fort Hare, South Africa.

Hesselbarth, M.H.K., Wiegand, K., Dreber, N., Kellner, K., Esser, D. and Tsvuura, Z. 2018. Density-dependent spatial patterning of woody plants differs between a semi-arid and a mesic savanna in South Africa. *Journal of Arid Environments* 157:103-112.

IUSS Working Group WRB. 2014. World Reference Base for Soil Resources 2014: international soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports no. 106.

Jordaan, J.J. 2010. The proposed colonisation sequence of woody species in the Sourish Mixed Bushveld of the Limpopo province. *South Africa. African Journal of Range & Forage Science* 27:105-108.

Joubert, D.F., Rothauge, A., Smit, G.N., 2008. A conceptual model of vegetation dynamics in the semiarid Highland savanna of Namibia, with particular reference to bush thickening by *Acacia mellifera*. *Journal of Arid Environment* 72:2201-2210.

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.

Kraaij, T. and Ward, D. 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant ecology* 186:235-246.

Lesoli, M.S., Gxasheka, M., Solomon, T.B. and Moyo, B. 2013. Integrated Plant Invasion and Bush Encroachment Management on Southern African Rangelands. Herbicides: Current Research and Case Studies in Use. INTECH 259-313.

Magurran, A.E. 2004. Measuring biological diversity. Blackwell Science Publishers.

Meik, J.M., Jeo, R.M., IIIa, J.R.M. and Jenks, K.E. 2002. Effects of bush encroachment on an assemblage of diurnal lizard species in central Namibia. *Biology Conservation* 106:29-36.

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.

Moleele, N.M., Ringrose, S., Matheson, W. and Vanderpost, C. 2002, ‘More woody plants? The status of bush encroachment in Botswana’s grazing areas’. *Journal of Environmental Management* 64: 3-11.

Mucina, L. and Rutherford, M.C. 2006. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute.

Munjonji, L., Ayisi, K.K., Vanderwalle, B., Haesaert, G. and Boekx, P. 2016. Combining carbon-13 and oxygen-18 to unravel triticale grain yield and physiological response to water stress. *Field Crops Research* 195:36-49.

O'Connor, T.G. and Crow, V.R.T. 1999. Rate and pattern of bush encroachment in Eastern Cape savanna and grassland. *African Journal of Range and Forage Science* 16:26-31.

Roques, K.G., O’connor, T.G and Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of applied ecology* 38:268-280.

Scholes, R.J., and Archer, S.R. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28:517-544.

Shackleton, C. M. and Gambiza, J. 2008. Social and ecological trade-offs in combating land degradation: The case of invasion by a woody shrub (*Euryops floribundus*) at Macubeni, South Africa. *Land Degradation and Development*, 19, 454–464.

Soil Classification Working Group. 1991. Soil classification: a taxonomic system for South Africa. Department of Agricultural Development: Pretoria.

Tefera, S., Dlamini, B.J. and Dlamini, A.M. 2008. Dynamics of Savannas in Swaziland: Encroachment of Woody Plants in Relation to Land Use and Soil Classes and Indigenous Knowledge on Plants Utilization. *Research Journal of Botany 3:49-64.*

Tessema, Z.K., Ejigu, B and Nigatu, L. 2017. Tree species determine soil seed bank composition and its similarity with understory vegetation in semi-arid African savanna. *Ecological processes* 6:9. DOI 10.1186/513717-017-0075-7.

Trollope W.S.W. 1980. Controlling bush encroachment with fire in the savanna areas of South Africa. Proceedings of Grassland Society of Southern Africa 15: 173-177.

Trollope, W.S.W., Potgieter, A.L.F and Zambatis, N. 1989. Assesing veld conditions in the Kruger National Park using key grass species. *Koedoe* 32:67-93.

Van Auken, O. W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management* 90:2931-2942.

Ward, D. 2005. Do we understand the causes of bush encroachment in African savannas? *African Journal of Range and Forage Science* 22:101-105.

Wiegand, K., Ward, D. and Saltz, D. 2005. Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer*. Journal of Vegetation Science* 16: 311-320.

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 a 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

$$BC = 19.8 + 0.39\,(D) - 11.87\,(logeD) + 0.64\,(d) + 2.93\,(loged). \qquad \text{(Eq. 1)}$$

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.

$$R = S \qquad \text{(Eq. 2)}$$

$$E = \frac{H}{InS} \qquad \text{(Eq. 3)}$$

$$H' = \sum_{i=1}^{S} (p_i Inp_i) \qquad \text{(Eq. 4)}$$

Where H is the Shannon-Wiener index (the measure of species diversity), p_i is the weight proportion of total number of species, *In* 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 aperture 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_4HCO_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 bushencroached 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.

Species	**Life form**	**Ecological value**	**Open**	**Intermediate**	**Intensive**
Relative abundance (%)					
Arista congesta	WP	Inc II	0.8	0.5	-
Brachiaria nigropedata	P	Dec	4	0.3	-
Cynodon dactylon	WP	Inc	4	5	2
Digiteria eriantha	P	Dec	7	16	-
Eragrostis lehmanniana	P	Inc II	-	5	5
Eragrostis rigidior	WP	Inc II	60	24	3
Eragrostis superba	WP	Inc II	0.2	24	-
Heteropogon contortus	P	Inc II	2	8	4
Melinis repens	WP	Inc II	-	0,.7	-
Panicum maximum	P	Dec	-	8	90
Panicum natalense	P	Inc II	2	1	-
Pogonarthria squarossa	WP	Inc II	-	0,3	-
Schmidtia pappophoroides	P	Dec	18	5	-
Themeda triandra	P	Dec	2	0.01	-

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.

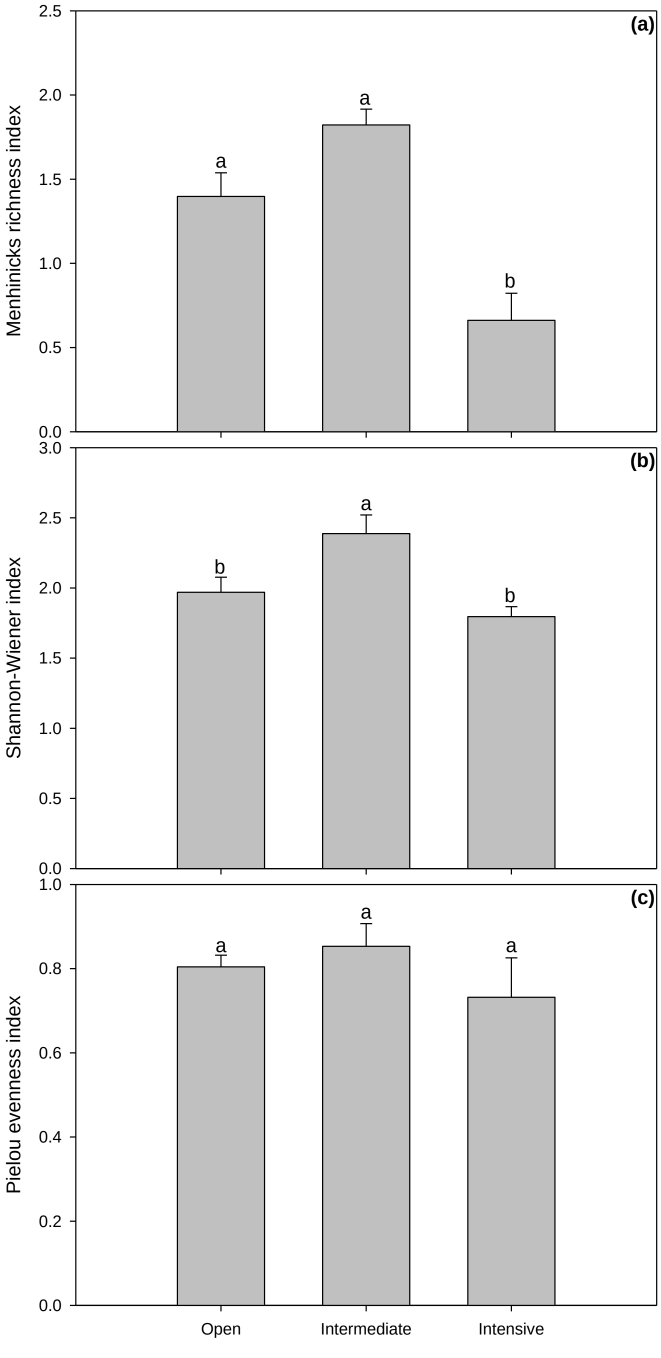

Figure 4.2. Comparison of grass richness index (a), Shannon-Wiener index (b) and Pielou's evenness index in open, intermediate and intensive bush-encroached grassland. The value is the mean ± standard error obtained from six plots in each encroachment level. Different letters above the bars indicate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

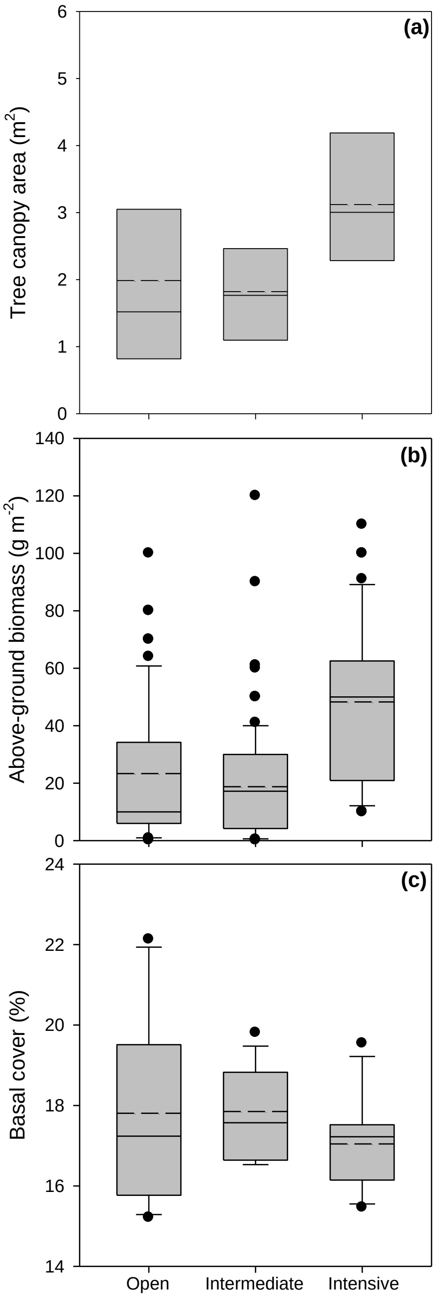

Figure 4.3. Distribution of tree canopy area (a), above-ground biomass (b) and basal cover (c). Graphic is based on six plots per encroachment level and is depicted using box plots with whiskers extending from the 25th and 75th percentile, median marked with black horizontal line across the box.

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.

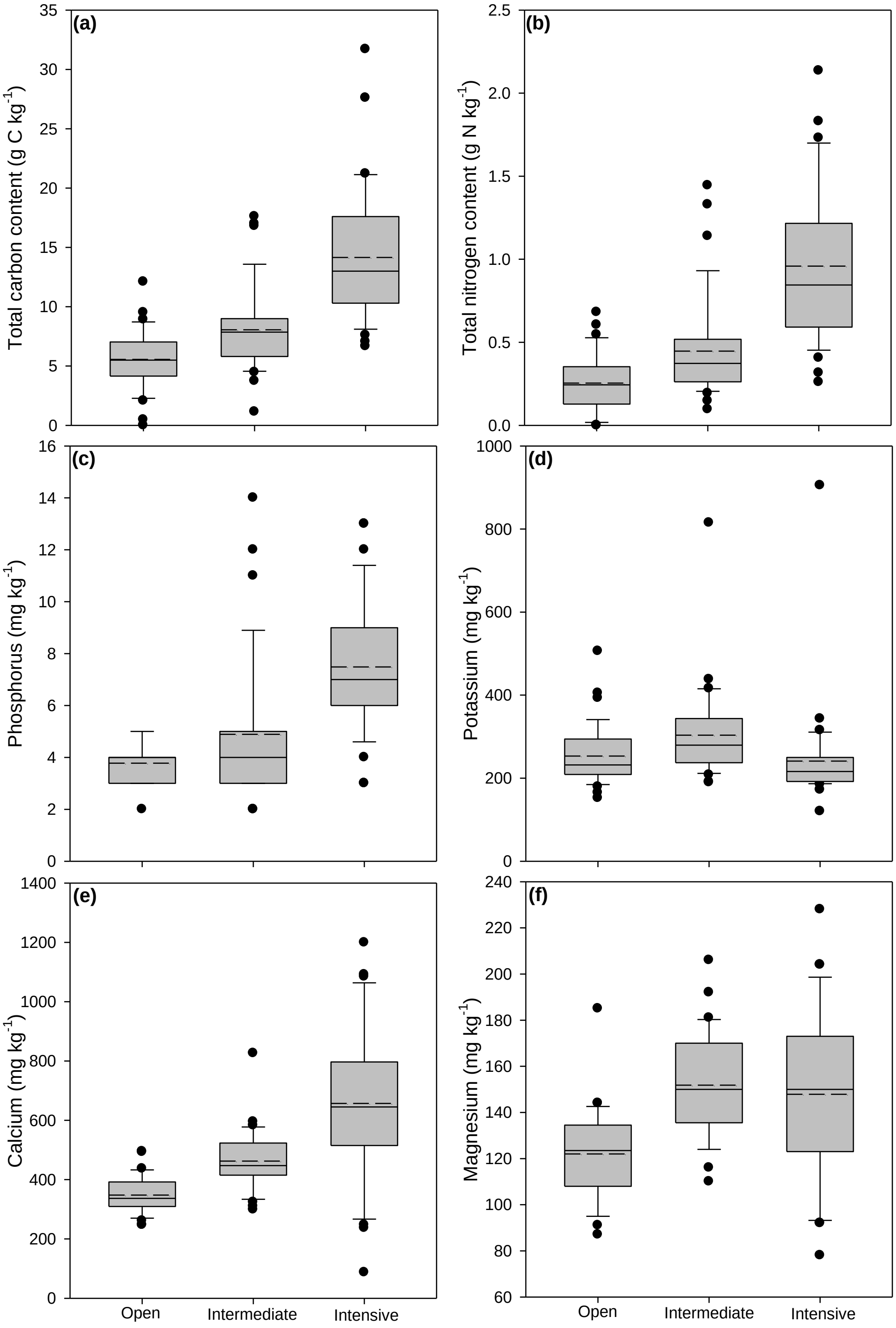

Figure 4.4. Topsoil (0-5 cm) distribution of (a) total carbon content (b) total nitrogen content (c) phosphorus (d) potassium (e) calcium and (f) magnesium in open, intermediate and intensively bush-encroached rangeland using box plots, with whiskers extending from the 25th and 75th percentile, median 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).

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.

Open	TH	LCD	SCD	LBH	TCA	TR	TSD	TE	BC	GR	GSD	GE
TH	1.00											
LCD	0.70	1.00										
SCD	0.47	0.88	1.00									
LBH	0.42	0.30	0.20	1.00								
TCA	0.87	0.61	0.81	0.31	1.00							
TR	0.34	0.64	0.41	-0.26	-0.05	1.00						
TSD	-0.56	-0.49	-0.51	-0.87	-0.64	0.07	1.00					
TE	-0.46	-0.28	-0.41	-0.87	-0.58	0.36	0.95	1.00				
BC	-0.12	-0.17	-0.18	-0.35	0.14	0.93	-0.26	0.02	1.00			
GR	-0.97	-0.89	-0.96	0.10	-0.81	-0.46	0.36	0.18	-0.57	1.00		
GSD	-0.84	-0.85	-0.89	-0.15	-0.63	-0.20	0.58	0.52	-0.50	0.75	1.00	
GE	-0.66	-0.41	-0.61	0.22	-0.66	0.26	0.12	0.20	0.14	0.64	0.65	1.00
Intermediate	TH	LCD	SCD	LBH	TCA	TR	TSD	TE	BC	GR	GSD	GE
TH	1.00											
LCD	0.33	1.00										
SCD	0.36	0.87	1.00									
LBH	0.11	0.43	0.38	1.00								
TCA	0.43	-0.3	-0.25	-0.74	1.00							
TR	-0.05	0.19	0.31	0.24	-0.02	1.00						
TSD	-0.08	0.72	0.81	0.54	-0.26	0.8	1.00					
TE	-0.06	0.51	0.61	0.43	-0.12	0.94	0.95	1.00				
BC	-0.13	-0.17	-0.25	0.04	-0.11	-0.76	-0.57	-0.66	1.00			
GR	0.81	-0.25	-0.52	0.08	0.17	0.05	-0.24	-0.1	0.28	1.00		
GSD	-0.72	-0.18	0.11	-0.04	-0.51	0.31	0.26	0.24	-0.66	-0.52	1.00	
GE	-0.93	-0.11	0.2	-0.03	-0.41	0.3	0.28	0.28	-0.59	-0.76	0.90	1.00
Intensive	TH	LCD	SCD	LBH	TCA	TR	TSD	TE	BC	GR	GSD	GE
TH	1.00											
LCD	0.58	1.00										
SCD	0.32	0.61	1.00									
LBH	0.52	0.51	0.48	1.00								
TCA	-0.31	-0.67	-0.69	-0.80	1.00							
TR	-0.48	0.21	0.26	0.74	-0.66	1.00						
TSD	-0.47	0.29	0.34	0.71	-0.55	0.94	1.00					
TE	-0.61	0.15	0.19	0.72	-0.43	0.94	0.89	1.00				
BC	-0.02	-0.22	-0.17	0.28	-0.20	0.34	0.15	0.19	1.00			
GR	-0.36	-0.54	-0.57	-0.56	0.42	-0.08	0.02	-0.12	-0.04	1.00		
GSD	-0.51	-0.30	-0.30	-0.31	0.62	-0.06	0.21	0.11	-0.36	0.64	1.00	
GE	-0.38	0.40	0.44	0.77	-0.26	0.66	0.70	0.84	-0.22	-0.39	0.19	1.00

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.

The first and second axes of the PCA explained 50% and 21% of the total variance of soil nutrients and vegetation parameters in open grassland (Figure 4.5; Table 4.3). Exchangeable Ca, Mg, P and TSD were the main contributors to first axis (PC_1). TR was the main contributor to the second axis (PC_2). In intermediate bush-encroached grassland, (PC_1) explained 46% of the total data variation, and main contributors were exchangeable Mg, P, Ca, GE and GSD. PC_2 which explained 21% of the data variation was related to TR. In intensive bush-encroached grassland, (PC_1) which explained 47% of the data variation was related to total C, N opposed GE. PC_2 was related to GSD, GR opposed to TH and P.

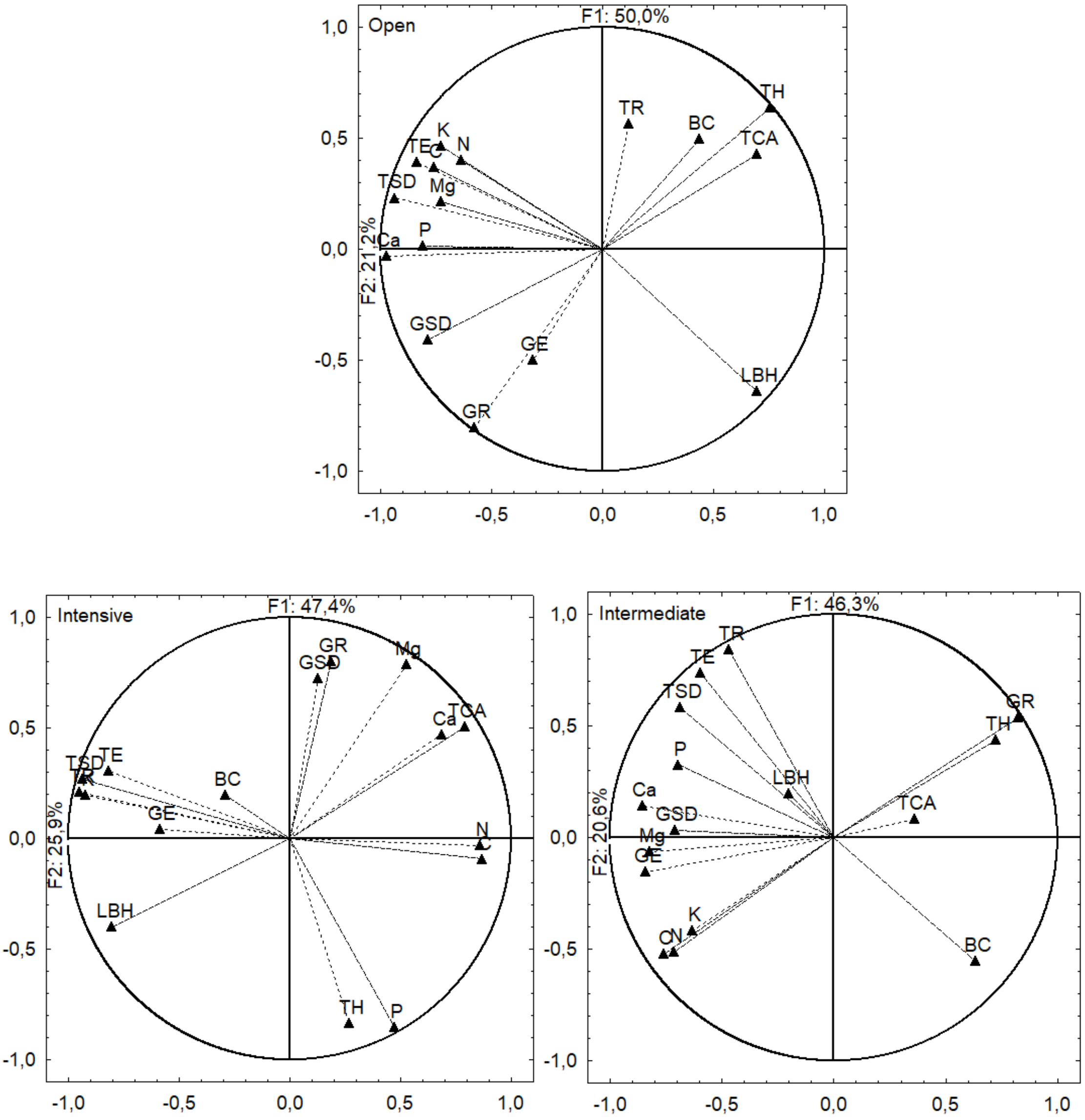

Figure 4.5: Principal component analysis of selected soil properties and vegetation components along different encroachment gradients in a savanna rangeland. Note: TH- tree height, LCD- longest crown diameter, SCD- shortest crown diameter, LBH- lowest browsable height, TR - tree richness, TSD - tree 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.

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

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 is 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

Aweto, A.O. and Dikinya, O. 2003. The beneficial effects of two tree species on soil properties in a semi-arid savanna rangeland in Botswana. *Land Contamination & Reclamation* 11:339-344.

Bakker, J.P., Hoffmann, F., Ozinga, W.A. and Rosen, E. 2014. Shading results in depletion of the soil seedbank. *Nordic Journal of Botany* 32:674-679.

Belayneh, A. and Tessema, Z.K. 2017. Mechanisms of bush encroachment and its inter-connection with rangeland degradation in semi-arid African ecosystems: a review. *Journal of Arid Land* 9:299-312.

Belsky, A.J., Amundson, R.G., Duxbury, J.M., Riha, S.J., Ali, A.R. and Mwonga, S.M. 1989. The effects of trees on their physical, chemical and biological environment in a semi-arid savanna in Kenya. *Journal of Applied Ecology* 26:1005-1024.

Bernhard-Reversat, F. 1982. Biogeochemical cycle of nitrogen in semi-arid savanna. *Oikos* 38:321-332.

Binkley, D. 1994. The influence of tree species on forest soils: processes and patterns. *Proceedings of the trees and soil workshop* 1-33.

Bouyoucos, G.J. 1962. Hydrometer method improved for making particle size analyses of soils 1. *Agronomic Journal* 54:464-465.

Brantley, S.T. and Young, D.R. 2007. Leaf-area index and light attenuation in rapidly expanding shrub thickets. *Ecology* 88:524-530.

Briggs, J.M., Knapp, A.K., Blair, J.M., Heisler, J.L., Hoch, G.A., Lett, M.S. and McCarron, J.K. 2005. An ecosystem in transition. Causes and consequences of the conversion of mesic grassland to shrubland. *Bioscience* 55: 243-254.

Devine, A.P., McDonald, R.A., Quaife, T. and Maclean, I.M.D. 2017. Determinants of woody encroachment and cover in African savannas. *Oecologia* 183:939-951.

Dlamini, P., Mbanjwa, V., Gxasheka, M., Tyasi, L. and Sekhohola-Dlamini, L. 2019. Chemical stabilisation of carbon stocks by polyvalent cations in plinthic soil of a shrub-encroached savanna grassland. *Catena* 181:104088.

Dye, P.J. and Spear, P.T. 1982. The effects of bush clearing and rainfall variability on grass yield and composition in south-west Zimbabwe. *Journal of Agricultural Research* 20:103-118.

Eldridge, D.J. and Soliveres, S. 2014. Are shrubs really a sign of declining ecosystem function? Disentangling the myths and truths of woody encroachment in Australia. *Australian Journal of Botany* 62:594-608.

Gobelle, S.K. and Gure, A. 2018. Effects of bush encroachment on plant composition, diversity and carbon stock in Borana rangelands, Southern Ethiopia. *International Journal of Biodiversity and Conservation* 10:230-245.

González-Roglich, M., Swenson, J.J., Jobbágy, E.G. and Jackson, R.B. 2014. Shifting carbon pools along a plant cover gradient in woody encroached savannas of central Argentina. *Forest Ecology and Management* 331:71-78.

Guido, A., Salengue, E. and Dresseno, A. 2017. Effect of shrub encroachment on vegetation communities in Brazilian forest-grassland mosaics. *Perspectives in ecology and conservation* 15:52-55.

Hardy, M.B. and Tainton, N.M. 1993 Towards a technique for determining basal cover in tufted grasslands. *African Journal of Range and Forage Science* 10:77-81.

Hesselbarth, M., Wiegand, K., Dreber, N., Kellner, K., Esser, D. and Tsvuura, Z. 2018. Density-dependent spatial patterning of woody plants differs between a semi-arid and a mesic savanna in South Africa. *Journal of Arid Environments* 157:103-112.

Holdo, M.R. and Mack, M. 2014. Functional attributes of savanna soils: contrasting effects of tree canopies and herbivores on bulk density, nutrients and moisture dynamics. *Journal of Ecology* 102:1171-1182.

Hutchinson, T.F., Boerner, R.A.J., Iverson, L.R., Sutherland, S. and Kennedy Sutherland, E. 1999. Landscape patterns of understory composition and richness across a moisture and nitrogen mineralization gradient in Ohio (USA) Quercus forests. *Plant Ecology* 144:177-189.

Kennard, D.G. and Walker, B.H. 1973. Relationships between tree canopy cover and Panicum maximum in the vicinity of Fort Victory. *Rhodesian Journal of Agricultural Research* 11:145-153.

Légaré, S., Bergeron, Y., Leduc, A. and Pare´, D. 2001. Comparison of the understory vegetation in boreal forest types of southwest Quebec. *Canadian Journal of Botany* 79:1019-1027.

Li, H., Shen, H., Chen, L., Liu, T., Hu, H., Zhao, X., Zhou, L., Zhang, P. and Fang, J. 2016. Effects of shrub encroachment on soil organic carbon in global grasslands. *Scientific reports* 6:28974.

Liu, F., Wu, X. B., Bai, E., Boutton, T.W. and Archer, S.R. 2011. Quantifying soil organic carbon in complex landscapes: an example of grassland undergoing encroachment of woody plants. *Global Change Biology* 17:1119-1129.

Maestre, F.T., Bowker, M.A., Puche, M.D., Belén Hinojosa, M., Martínez, I., García-Palacios, P., Castillo, A.P., Soliveres, S., Luzuriaga, A.L. and Sánchez, A.M. 2009. Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. *Ecology Letters* 12:930-941.

Magurran, A.E. 2004. Measuring biological diversity. Blackwell Science Publishers.

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.

Moustakas, A., Wiegand, K., Meyer, K.M., Ward, D. and Sankaran, M. 2010. Perspective: Learning new tricks from old trees: revisiting the savanna question. *Frontiers of biogeography* 2:47-53.

Mucina, L. and Rutherford, M.C. 2006. The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute.

Nunes Biral, V.C., Will, R.E. and Zou, C.B. 2019. Establishment of *Querus marilandica Muenchh.* And *Juniperus virginiana L*. in the Tallgrass Prairie of Oklahoma, USA Increases Litter Inputs and Soil Organic Carbon. *Forests* 10.329. Doi:10.3390/f10040329.

O'Connor, T.G., Puttick, J.R. and Hoffman, M.T. 2014. Bush encroachment in southern Africa: changes and causes. *African Journal of Range and Forage Science* 31:67-88.

Price, J.N. and Morgan, J.W. 2008. Woody plant encroachment reduces species richness of herb-rich woodlands in southern Australia. *Ecological Society of Australia* 33:278-289.

Ratajczak, Z., Nippert, J.B. and Collins, S.L. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology* 93:697-703.

Richter, C.G.F., Snyman, H.A. and Smit, G.N. 2001. The influence of tree density on the grass layer of three semi-arid savanna types of Southern Africa. *African Journal of Range and Forage Science* 18:103-109.

Sankaran, M., Jayashree, R. and Hanan, N.P. 2004. Tree-grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* 7:480-490.

Scholes, R.J., and Archer, S.R. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28:517-544.

Simmons, M.T., Archer, S.R., Teague, W.R. and Ansley, R.J. 2008. Tree (*Prosopis glandulosa*) effects on grass grass growth: An experimental assessment of above- and below ground interactions in a temperate savanna. *Journal of Arid Environments* 72:314-325.

Thompson, J.A., Zinnert, J.C. and Young, D.R. 2017. Immediate effects of microclimate modification enhance native shrub encroachment. *Ecosphere* 8:e01687.

Throop, H.L. and Lajtha, K. 2018. Spatial and temporal changes in ecosystem carbon pools following juniper encroachment and removal. *Biogeochemistry* 140:373-388.

Turnbull, L., Wainwright, J., Brazier, R.E. and Bol, R. 2010. Biotic and abiotic changes in ecosystem structure over a shrub-encroachment gradient in the Southwestern USA. *Ecosystems* 13: 1239-1255.

Turpin-Jelfs, T., Michaelides, K., Biederman, J.A. and Anesio, A.M. 2019. Soil nitrogen response to shrub encroachment in a degrading semi-arid grassland. *Biogeosciences* 16:369-381.

van Oudtshoorn, F. 2014. Guide to Grasses of Southern Africa. Briza Publication, Pretoria, South Africa.

van Wyk, B., and van Wyk, P. 1997. Field guide to trees of Southern Africa. Struik Publishers, Cape Town, South Africa.

Veetas, O.R. 1992. Micro-site effects of trees and shrubs in dry savannas. *Journal of Vegetation Science* 3:337-344.

Venter, Z., Cramer, M. and Hawkins, H. 2018. Drivers of woody plant encroachment over Africa. *Nature communications* 9:2272. DOI: 10.1038/s41467-018-04616-8.

Wang, G., Li, J., Ravi, S., Theiling, B.P. and Sankey, J.B. 2019. Fire changes the spatial distribution and sources of soil carbon in a grassland-shrubland transition zone. *Plant and Soil* 435:309-321.

Ward, D., Trinogga, J., Wiegand, K., du Toit, J., Okubamichael, D., Reinsch, S. and Schleicher, J. 2018. Large shrubs increase soil nutrients in a semi-arid savanna. *Geoderma* 310:153-162.

Webster, R. 2001. Statistics to support soil research and their presentation. *European Journal of Soil Science* 52:331-340.

Weintraub, M.N. and Schimel, J.P. 2005. Nitrogen cycling and the spread of shrubs control changes in carbo balance of Arctic Tundra ecosystems. *BioScience* 55: 408-415.

Wiegand, K., Saltz, D. and Ward, D. 2006. A patch-dynamics approach to savanna dynamics and woody plant encroachment - Insights from an arid savanna. *Perspectives in Plant Ecology, Evolution and Systematics* 7:229-242.

Wiegand, K., Ward, D. and Saltz, D. 2005. Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer. *Journal of Vegetation Science* 16:311-320.

Wilcox, B.P., Birt, A., Fuhlendorf, S.D. and Archer, S.R. 2018. Emerging frameworks for understanding and mitigating woody plant encroachment in grassy biomes. *Current Opinion in Environmental Sustainability* 32:46-52.

Wright, A., Schnitzer, S.A., Dickie, I.A., Gunderson, A.R., Pinter, G.A., Mangan, S.A. and Reich, P.B. 2013. Complex facilitation and competition in a temperate grassland: loss of plant diversity and elevated CO_2 have divergent and opposite effects on oak establishment. *Oecologia* 171:449-458.

Zhou, L., Shen, H., Chen, L., Li, H., Zhang, P., Zhao, X., Liu, T., Liu, S., Xing, A., Hu, H. and Fang, J. 2019. Ecological consequences of shrub encroachment in the grasslands of northern China. *Landscape Ecology* 34:119-130.

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

Source of variation	df	Sum of squares	Mean square	F	P
Between groups	3	84.744	28.248	0.904	0.448
Within groups	41	1281.841	31.264		
Total	44	1366.585			

Grass species richness

Source of variation	df	Sum of squares	Mean square	F	P
Between groups	2	4.143	2.071	19.02	0
Within groups	15	1.633	0.109		
Total	17	5.776			

Grass species diversity

Source of variation	df	Sum of squares	Mean square	F	P
Between groups	2	1.109	0.555	8.093	0.004
Within groups	15	1.028	0.069		
Total	17	2.137			

Grass species evenness

Source of variation	df	Sum of squares	Mean square	F	P
Between groups	2	0.44	0.022	0.894	0.43
Within groups	15	0.373	0.025		
Total	17	0.418			

Tree species richness

Source of variation	df	Sum of squares	Mean square	F	P
Between groups	2	0.775	0.387	4.093	0.038
Within groups	15	1.42	0.095		
Total	17	2.195			

Tree species diversity

Source of variation	df	Sum of squares	Mean square	F	P
Between groups	2	1.0.15	0.508	4.353	0.032
Within groups	15	1.75	0.117		
Total	17	2.765			

Tree species evenness

Source of variation	df	Sum of squares	Mean square	F	P
Between groups	2	0.275	0.137	4.986	0.022
Within groups	15	0.414	0.028		
Total	17	0.689			

Tree Height

	df	Sum of Squares	Mean Square	F	P
Between Groups	2	137.136	68.568	25.71	0
Within Groups	159	424.06	2.667		

Total	161	561.197			

Longest Crown Diameter

	df	Sum of Squares	Mean Square	F	P
Between Groups	2	17.625	8.813	6.641	0.002
Within Groups	159	211.001	1.327		
Total	161	228.627			

Shortest Crown Diameter

	df	Sum of Squares	Mean Square	F	P
Between Groups	2	15.332	7.666	6.161	0.003
Within Groups	159	197.821	1.244		
Total	161	213.152			

Lowest Browsable Height

	df	Sum of Squares	Mean Square	F	P
Between Groups	2	16.528	8.264	7.2	0.001
Within Groups	159	182.503	1.148		
Total	161	199.031			

Appendix 2: One-way analysis of variance for soil properties in open, intermediate and intensive bush encroached savanna grassland.

Total C

	Sum of Squares	df	Mean Square	F	P
Between Groups	1246.482	2	623.241	34.774	.000
Within Groups	1863.961	104	17.923		
Total	3110.443	106			

Total N

	Sum of Squares	df	Mean Square	F	P
Between Groups	6.558	2	3.279	17.600	.000
Within Groups	18.818	101	.186		
Total	25.376	103			

Soil P

	Sum of Squares	df	Mean Square	F	P
Between Groups	244.380	2	122.190	26.126	.000
Within Groups	486.405	104	4.677		
Total	730.785	106			

Soil Mg

	Sum of Squares	df	Mean Square	F	P
Between Groups	17917.454	2	8958.727	12.433	.000
Within Groups	74935.294	104	720.532		
Total	92852.748	106			

Soil K

	Sum of Squares	df	Mean Square	F	P
Between Groups	84809.433	2	42404.717	4.011	.021
Within Groups	1099570.753	104	10572.796		
Total	1184380.187	106			

Soil Ca

	Sum of Squares	df	Mean Square	F	P
Between Groups	1535285.129	2	767642.564	26.781	.000
Within Groups	2981035.918	104	28663.807		
Total	4516321.047	106			