Effects of Nitrogen Fertilization and Precipitation Decline on Tree-Grass Interactions in Southern African Savannas

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R013318R

Thesis submitted to the Department of Geography and Environmental Science in partial fulfillment of the requirements for the Doctor of Philosophy degree in Geography and Environmental Science (Spatial Ecology)

June 2018

UNIVERSITY OF ZIMBABWE

Abstract

Savannas are heterogeneous ecosystems comprising of a co-dominance of herbaceous and woody species and these ecosystems support millions of people as well as diverse mammalian species. Recent research has established that savannas are undergoing structural changes mainly characterised by an increase in the woody component commonly referred to as woody encroachment. However, this widespread phenomenon is still poorly understood. This study sought to fill this gap by using innovative wavelet based methods to test the existence of this phenomenon as well as quantify its extent. Using a four year field experiment and satellite data the study tested whether and to what extent woody encroachment is explained by variations in key resources, that is, moisture availability and nitrogen. In the experiment, rainfall was reduced by 15% using fixed location rainout shelters while Nitrogen fertilizer was added as ammonium nitrate (NH_4NO_3) at a rate of 4 grams of N m^{-2} at the start of the rainfall season each year. As rainfall received at the study site varied across the study period, the amount of rainfall suppressed was variable with as little as 50 mm (for a rainfall total = 337 mm) in 2012 to as much as 125 mm in 2014 (for a rainfall total 832 mm). Results of wavelet analysis on multi-temporal imagery point towards an increase in woody encroachment thereby providing new insights into the phenomenon. For instance, at Lake Chivero where woody patches were already established the dominant scale of woody patches quadrupled over the 39-year period while the intensity decreased slightly by 0.7%. In contrast, at Kyle which was predominantly a grassland, the dominant scale decreased from 32 m to 16 m over the same period while intensity increased by >200%. Results further indicate that decadal changes in rainfall significantly explain woody patch dynamics in semi-arid savanna landscapes. In fact, decadal changes in rainfall significantly explained more than 85% of the variation in woody patch dynamics ($R^2 = 0.85$, $F_{13} = 35.9$, $P < 0.01$). In addition, results from field experiments indicate that moisture availability and its interaction with nitrogen had significant ($P<0.05$) but transient effects on woody species recruitment in a semi-arid savanna ecosystem using *Vachellia karroo* as a focal species. Though not significant, woody saplings growing under suppressed rainfall were, overall, 9% shorter (64.72±13.98cm SD) than the control (71.034±13.982cm SD). In contrast, saplings growing under rainfall suppression had a slightly larger diameter (1.153±0.348cm SD) than those growing in the control (1.056±0.418cm SD). However, grass competition did not significantly influence the growth of *V. karroo* species either alone or in interaction with nitrogen and rainfall. Future climate change projections indicate the bioclimatically suitable range of *V. karroo* in southern Africa will expand despite the projected rainfall decrease. Results of this thesis further the understanding of woody encroachment and its key drivers in a changing savanna environment.

Acknowledgements

This thesis would not have come to fruition were it not for the support of several individuals and organisations who not only provided the much needed mentorship , academic support but also financial resources throughout the duration of this study. First of all I would like to thank my supervisors Dr Masocha and Professor Murwira. Without your support I am sure this study would not have been successful. Your divergent but complementary views on science in general and scientific writing style in particular have taught me how to merge divergent views into a coherent storyline.

I wish to express my profound gratitude to Dr Masocha whose incisive and constructive criticism considerably shaped ideas presented in this thesis. You taught me the scientific method, especially hypothesis formulation and testing. I remember you saying "*Munya this is not a mechanistic hypothesis*". I hope this thesis provides evidence that I now understand a mechanistic hypothesis.

To Prof Murwira your philosophy on life has taught me that nothing is impossible as long as you are living. I will never forget the numerous discussions we had in your office in which you always focused on the positives when I felt overwhelmed not only with school but teaching obligations. The following bears testimony on the positive approach you always inculcate in people.

"By whatever means use the available opportunity to complete PhD......do extraordinary things.....don't be normal.........remember Sheks if you are not a lecturer you are a student therefore you don't have time to rest".

Indeed were it not for these hard talks, I am sure we wouldn’t be talking about this thesis. Most importantly Prof, you have taught me how to tease out scientific problems. Surely a PhD is like an elephant, you can’t eat it at one go, rather, it’s eaten one piece at a time. Ultimately, it get’s finished and you wonder how you managed to achieve that feat.

To “Dotore” , Zengeya, thank you for your critical comments that helped in refining my ideas. You were always available to give your insightful comments when requested to review my papers. Mr Gaza is thanked for nutrient testing in soil and plants.

My sincere gratitude to goes to Mr Christopher Chapano of Harare Botanical Gardens for assisting with fieldwork especially on botany. I remember at times you would come in the middle of night only to find me sleeping with 26 missed calls on my phone. Thanks for the patience and being a big brother.

Mr Gwitira, I will always be grateful for having a friend, workmate and a fellow scientist who would always provide a shoulder to lean on. You were always there to provide not only moral but technical as well as scientific advice regardless of the place. I will always cherish the chats we had on our way home and in the office. Indeed, you are more than a friend.

I would also want to thank the University of Zimbabwe for funding the experimental component of this study. Surely the funding assisted in making this study a success.

My sincere gratitude to the Surveyor General’s Office for providing aerial photographs used in this study. I would also want to thank the Parks and Wildlife Management Authority for allowing me to perform my experiment at Kyle Game Reserve. Heartfelt gratitude to David Tinago for fence erection and data collection at the experimental station.

Most importantly, I would really want to thank my family who endured so many lonely years to facilitate my completion of this thesis. Hopefully, after successfully completing this thesis, dad will always be available to all of you.

Dedication

To

my dearest wife Dorcas, and our children Tiana, Trenton and Talia

&

in memory of my mother and father who could not live to see me this far.

Declaration 1: Originality

I hereby declare that this thesis submitted for the Doctor of Philosophy degree in Geography and Environmental Science (Spatial Ecology) at the University of Zimbabwe is my original work and has not been previously submitted to any institution of higher education. I further declare that all sources cited or quoted are indicated by means of a comprehensive list of references.

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Munyaradzi Davis Shekede

Declaration 2: Publications

Details that form part and/or presented in this thesis include published articles and / or submitted manuscripts:

Publication 1: Munyaradzi D. Shekede[1], Amon Murwira[1] and Mhosisi Masocha[1] , 2015.

Wavelet-based detection of bush encroachment in a savanna using multi-temporal aerial photographs and satellite imagery. **International Journal of Applied Earth Observation and Geoinformation** 35 209–216

The work was conducted by the first author under the guidance and supervision of the second and third authors.

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Publication 2: Munyaradzi D. Shekede[1], Amon Murwira[1], Mhosisi Masocha[1] and Fadzai M Zengeya[1], 2016.

Decadal changes in mean annual rainfall drive long-term changes in bush-encroached southern African savannas. **Austral Ecology**, 41, 6,690-700

The work was conducted by the first author under the guidance and supervision of the second, third and fourth authors

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Publication 3: Munyaradzi D. Shekede[1], Amon Murwira[1] and Mhosisi Masocha[1]

Transitory effects of rainfall suppression and grass competition on the growth of *Vachellia karroo* sapling in a semi-arid southern African savanna (Paper submitted to the **African Journal of Ecology**).

The work was conducted by the first author under the guidance and supervision of the second and third authors.

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Publication 4: [1]Shekede, M.D., [1]Masocha, M. and [1]Murwira, A., 2018.

Transient effects of nitrogen addition and rainfall suppression on *Vachellia karroo* growth under grass competition in a southern African savanna. *Cogent Environmental Science*, *4*(1), p.1549799).

The work was conducted by the first author under the guidance and supervision of the second and third authors

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Publication 5: Munyaradzi D. Shekede[1], Mhosisi Masocha[1], Amon Murwira[1] and Gwitira I[1]

Spatial distribution of *Vachellia karroo* in Zimbabwean savannas (southern Africa) under a changing climate. *Ecological research*, *33*(6), pp.1181-1191.

The work was conducted by the first author under the guidance and supervision of the second and third authors. The fourth author helped with data analysis.

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Certification by Supervisors

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Table of contents

Chapter 7 Synthesis 161

List of Figures

List of Tables

Chapter 1 : General Introduction

1.1. The tree-grass co-existence problem

Whether studied from space or in the field, savanna ecosystems are distinctly observable by their two contrasting life forms, that is, trees and grasses that co-occur in the same landscape. This is despite the fact that some savannas are located in a humid subtropical climate that could potentially support closed forests (Bond, 2008). Exploring the mechanisms that explain this coexistence remains an unanswered question in Ecology and yet answering this question could aid conservation and sustainable management of these unique ecosystems (Scholes and Archer, 1997). Two models have been invoked to explain the co-existence of trees and grasses in savannas across the globe (Ward et al., 2013), that is, (1) competition-based models and (2) demographic models. Competition-based models explain tree-grass coexistence in terms of exclusive and differential access to resources, mainly water, by grasses and trees. This differential access to water results in greater within-life form competition than between-life form competition thereby promoting coexistence (Meyer et al., 2009). In other words, as grasses and trees exploit resources in exclusive zones, there is more tree to tree competition or grass to grass competition than between grasses and trees thereby promoting coexistence.

By contrast, demographic models emphasise bottle-necks in tree recruitment attributed to low moisture availability and disturbance factors, in particular fire and herbivory, to explain tree-grass coexistence (Higgins et al., 2000, Jeltsch et al., 1996, Van Langeveld et al., 2003). These main disturbance factors, for example, hot fires prevent trees from completely excluding grasses through topkill (Bond et al., 2003, Freeman et al., 2017) resulting in co-dominance with grasses in the same landscape (Cardoso et al., 2016, Sankaran et al., 2004). Once woody species have escaped the fire-trap, their suppressive effects on grasses become more enhanced but recurrent fires will again reduce woody biomass thereby limiting transition of savannas into a forest landscape.

Both experimental and theoretical studies have provided evidence for and against competition-based models and demographic models. For instance, competition-based models have been successfully used to explain tree-grass co-existence in African (Knoop and Walker, 1985, Ward et al., 2013), Australian (Fensham et al., 2005) and south American savanna ecosystems (Sala et al., 1989). In recent years, several studies have failed to find evidence in support of the competition-based models (Jeltsch et al. (1996), Wiegand et al., 2005, (Kulmatiski and Beard, 2013, Kulmatiski et al., 2017) especially in explaining woody encroachment, that is, an increase in woody cover at the expense of grass cover in savanna ecosystems (Archer, 1989, Hoffman and O'Connor, 1999, Wigley et al., 2009, Wigley et al., 2010, Wigley et al., 2009, Wigley et al., 2010). This is contrary to stable co-existence of these two life forms as predicted by competition-based models. In light of this increasing evidence against competition-based models, ecologists have sought alternative explanations for the co-existence of trees and grasses in savanna under the demographic model framework by either invoking fire (Higgins et al., 2000, Jeltsch et al., 1996, Jeltsch et al., 2000) or rainfall variability (Fensham et al., 2017). Overall, these studies suggest the existence of buffering mechanisms such as fire and herbivory that prevent savannas to transit into either a wholly grass-or tree-dominated ecosystem (Jeltsch et al., 2000). However, demographic bottleneck models have also failed to account for the increase in woody cover being experienced in savannas across the globe. Thus, additional mechanisms may be required to explain the increase in woody cover being experienced in savannas.

Although these two models (competition and demographic models) emphasize the relative importance of different mechanisms that is, competition for resources and tree recruitment limitation to explain tree-grass interactions and savanna structure, they both agree that two resources namely water and nitrogen (N) are critical. Both models assume a relatively stable environment that supplies predictable amounts of precipitation and N (Scholes and Archer, 1997). Yet, studies of global environmental changes have demonstrated that due to increased industrialization, combustion of fossil fuels, production of nitrogen fertilizers, and motorized traffic, rates of reactive N deposition to terrestrial ecosystems have increased (Bobbink et al., 2010, Phoenix et al., 2006, Valliere et al., 2017, WallisDeVries and Bobbink, 2017). N deposition i.e., the input of reactive nitrogen from the atmosphere to the biosphere occurs through gaseous and particulate transport (dry deposition) as well as via precipitation (wet deposition) (Clarke and Kremer, 2005). N is deposited in either oxidised form as nitric acid and particulate and aqueous nitrate (NO_3^-), or in reduced form as gaseous ammonia (NH_3), aerosol ammonium (NH_4^+) and wet deposited NH_4^+ (Kharol et al., 2018). Thus reactive N is absorbed by the leaf through the stomata while part of it is taken up by the roots in the soil solution after reaching the ground. At the global scale, it has been estimated that soil N levels rose from 35 $TgNyr^{-1}$ in the 19th century to 124 $TgNyr^{-1}$ in the 21st century (Fowler, 2004). This represents a 354% increase.

In southern African savannas, it has been reported that N deposition increased three to four fold between 1955 and 2003 (Scholes et al., 2003). The rates of deposition are expected to increase over the coming years (Dentener and Peuch, 2006, Phoenix et al., 2006, Sheffield and Wood, 2008) due to higher levels of fossil fuel consumption. N deposition is already having profound effects on ecosystems across the globe and the effects are likely to intensify in future.

1.2 Global Environmental changes: implications for savanna functioning

Considering that N is a key limiting resource in savannas, changes in N availability are likely to influence the competitive outcome between trees and grasses. Experimental evidence suggests that under increased N availability, grasses tend to be better competitors than trees in savannas due to root structural differences and growth attributes of these two life forms (Cohn et al., 1988, Cramer et al., 2010, van der Waal et al., 2009). This prediction is inconsistent with several correlative studies that report widespread woody encroachment in African (Archer, 1989, Roques et al., 2001, Skarpe, 1992, Wigley et al., 2009, Wigley et al., 2010), Australian (Bowman et al., 2001, Fensham and Fairfax, 2003, Fensham et al., 2005), North American (Archer, 1989, Asner et al., 2003), South American (Adamoli et al., 1990, Silva et al., 2001) and Asian (Singh and Joshi, 1979) savannas. One of the mechanisms invoked to explain the widespread woody encroachment by N-fixers is their ability to fix N thereby conferring them competitive advantage over non-fixers in nutrient poor environments as well contributing to soil N-economy. Perhaps, such conflicting evidence imply that N interact in a complex way with other factors such as moisture availability to mediate tree-grass interactions and the trajectory of change hence this warrants further investigation.

Concurrent with observed changes in N deposition rates to ecosystems, precipitation is predicted to change by different magnitudes and in different directions (IPCC 2007). In West and East Africa, several global models indicate a wetter climate by the end of the 21st century. A drying trend is projected for northern and southern Africa (except for the Eastern part of South Africa) under high emission scenarios (IPCC, 2014a). Although uncertainty among rainfall projections for southern Africa is high, rainfall is generally projected to decrease by between 10 and 30% (IPCC, 2014, Serdeczny et al., 2017) in this region. It is still not clear how the decrease in precipitation, which varies in magnitude, may alter the competitive milieu of trees and grass in southern Africa savannas. Considering that widespread tree recruitment has been observed to coincide with wet episodes (Holmgren and Scheffer, 2001, Joubert et al., 2008), a drying trend may further suppress tree recruitment thus favouring grasses as predicted by demographic models. However, the widespread increase in woody cover implies other variables such as global CO_2 fertilisation (Archer et al., 1995, Bond et al., 2003, Buitenwerf et al., 2012, Kgope et al., 2010) interact with changes in resource ability to determine tree-grass ratios in savanna ecosystems.

It is however likely that a 30% precipitation decrease may have negligible effect on the outcome of tree-grass interactions in mesic savanna since these savannas are on the upper end of the precipitation gradient (Sankaran et al., 2005). Thus, a 30% precipitation decrease would be within the tolerance levels of grasses and trees found therein. Since arid savannas (with a mean annual precipitation of <350 mm) are at the lower end of the precipitation gradient, it can be hypothesised that a precipitation decrease of up to 30% may significantly alter the outcome of tree-grass interactions in favour of grasses due to their fast response to low and erratic rainfall patterns. At the same time, if the niche separation holds, trees, which are able to access water from deeper layers may be favoured by the projected decrease in rainfall over southern Africa. A further complication is that the response of these two life forms to changes in precipitation may be contingent on N availability. Given the predicted changes in precipitation and N, it is not clear whether the savanna will remain as we know it today or may undergo some fundamental structural and functional changes. Thus, there is need to gain a mechanistic understanding of the interactive effects of water and nitrogen availability on tree-grass interactions. Such knowledge is critical for the management of this ecosystem as it harbours the largest diversity of mammalian species and supports the lives of more than 400 million people in Africa who depend mostly on natural resources for their livelihoods (Sankaran et al., 2005). Moreover, while savannas account for a fifth of the terrestrial surface (Scholes and Archer, 1997), they contribute up to 30 % to global net primary production (Grace et al., 2006).

The combined effects of these global environmental change drivers on tree-grass interactions are poorly understood for savannas (Scholes and Walker, 1993). Based on how tree-grass interactions may change as a result of increases in N deposition and predicted decreases in precipitation, the thesis predicts that an increase in N coupled with a precipitation reduction may favour grasses due to their ability to exploit resources from the top soil layer (O'Connor, 1985). It is possible that with N enrichment, nitrogen fixer tree may out-compete grasses since they would exploit readily available N thus allocating more energy to growth than N fixation (Fox-Dobbs et al., 2010). Previous studies have shown that nitrogen fixers growing in N rich environments can allocate more energy to growth and reproduction than those in nutrient poor environments (Brody et al., 2010, Fox-Dobbs et al., 2010). Based on observational and experimental data Brody et al., (2010) found that *Acacia drepanolobium* (now known as *Vachellia drepanolobium*) trees growing in N-rich soils were more likely to reproduce than those in nutrient poor environments in an East African savanna. At the same study site, *Vachellia drepanolobium* growing on nutrient-rich soils preferentially utilized soil-based nitrogen sources instead of fixed nitrogen (Fox-Dobbs et al., 2010). Whether trees or grasses will be favoured in the future will depend on the competitive ability of these two life forms under an environment characterised by changes in resources such as decreases in rainfall and nitrogen enrichment. Savannas may transit into any one of the two states but this is dependent on the competitive ability of these two life forms under projected decreases in rainfall and nutrient enrichment as illustrated in Figure 1.1. With changes in nutrient and moisture availability savannas may (a) maintain a stable tree-grass co-existence or (b) or may shift towards a grass-dominated state or (c) a woody state. Thus, this research aimed at understanding the competitive outcome of trees and grasses under a changing environment.

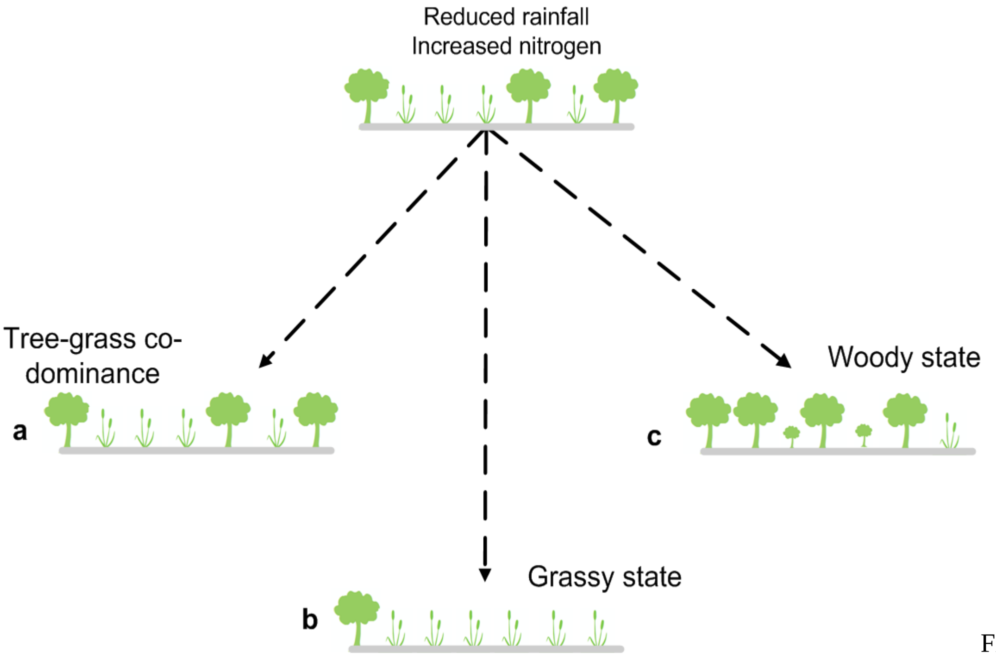

Figure 1.1: Conceptual model showing the potential states of savannas in response to changes in rainfall and nitrogen (N) availability. With changes in nutrient and moisture availability savannas may (a) maintain a stable tree-grass co-existence or (b) may shift towards a grass-dominated state or (c) a woody state.

1.3 Woody encroachment in savannas

So far studies have shown that savannas are undergoing structural changes characterised by an increase in trees and shrubs at the expense of grasses and herbs in a process known as woody encroachment (Moleele, 2002). Woody encroachment is often associated with a reduction in carrying capacity of rangelands (Negasa et al., 2014), changes in biogeochemical cycles (Wang et al., 2018), biodiversity loss (Devine et al., 2017, Price and Morgan, 2008, Ratajczak et al., 2012) and has profound effects on the livelihooods of people who are depedent on livestock production (Negasa et al., 2014). Although woody encroachment is a global phenomenon, little is known about the dynammics and mechanisms driving this process (Archer et al., 2017, Devine et al., 2017, Ward, 2005). The hypothesised drivers of woody encroachment include global ones such as rainfall variability, CO_2 enrichment, nutrient availability as well as local ones such as changes in fire regimes and herbivory (Van Auken, 2009). The lack of unequivocal evidence regarding mechanisms driving woody encroachment could be attributed to lack of methods that objectively quantify this ecological process. For instance, Wigley et al., (2009) relied on classification of aerial photographs to track changes in tree-grass ratios in Hluhluwe-Imfolozi Game Reserve of South Africa. Similarly, Buitenwerf et al., (2012a) used a combination of field surveys and multi-resolution segmentation and classification to estimate rates of woody encroachment in Kruger National Park .In another study, Odindi et al (2016a) perfomed random forest classification on high resolution satellite imagery to identify alien and indigenous encroacher species in a South African savanna. While these methods have provided estimates of woody encroachment, they neither provide estimates of densification nor the scale at which woody encroachment is occurring. This is despite the scale dependency nature of ecological processes such as woody encroachment. Thus, there is need to develop methods that can objectively characterise woody encroachment in terms of expansion or contraction of woody patches, densification as well as the scale of encroachment.

1.4 Problem statement

The understanding of the key mechanisms underlying structural changes in savannas could be improved through development of innovative methods that objectively characterise these structural changes. In this regard, previous attempts at estimating woody encroachment have mainly adopted traditional approaches that include field surveys (Yuan, 2005), visual interpretation of repeat fixed point photographs (Ward et al., 2014) and aerial photographs (Hudak and Wessman, 2001). While these approaches have provided evidence of woody encroachment, they require intensive field work and are susceptible to human error (Shekede et al., 2015). In addition, these traditional methods fail to determine the scale at which woody species encroachment occurs despite the intrinsic scale dependence of ecological processes such as woody encroachment (Wiegand et al., 2006, Wiens, 1989). Thus, there has been an increasing interest by ecologists to develop and apply innovative methods that harness latest geospatial technologies to objectively quantify the scale dependency of ecological pro-cesses. In this regard variograms (He et al., 2006) and wavelets have been applied to determine the spatial scale of vegetation structure in grasslands (He et al., 2007) and savannas (Strand et al., 2008, Strand et al., 2006). However, few of these studies have applied a framework that simultaneously characterises magnitude of changes in woody cover and linear dimensions of patches (Murwira and Skidmore, 2005a, Pittiglio et al., 2011). This has hampered the objective characterisation of structural changes in vegetation in savanna ecosystems that have a multi-scale structure. Thus, this study contributes to the understanding of woody patch dynamics through the use of innovative wavelet-based methods to test the existence of woody encroachment as well as quantify its extent by integrating satellite imagery and aerial photographs for several savanna sites in Zimbabwe. Furthermore, the present work tested the relationship between dynamics in woody species encroachment and rainfall variability across a rainfall gradient using a regression-based approach. To gain understanding on tree-grass interactions under global environmental change, the study also experimentally tests the effects of rainfall suppression and N addition on the growth of *Vachellia karroo* (*formerly known as Acacia karroo*), a common woody species in southern African savannas. Structural changes in savannas may affect their ability to provide goods and services e.g., an increase in woody component in savannas may reduce carrying capacity of rangelands and other services derived there from. Finally, ecological niche modelling using Maximum Entropy was applied to evaluate the potential effects of climate change on the distribution of *V. karroo*.

1.5 Research objectives

The main objective of the study was to understand whether and in what direction rainfall suppression and nitrogen addition alter tree-grass interactions in semi-arid southern African savannas. This thesis addresses five objectives. These were to:

(1) develop a framework for characterising woody encroachment in savannas based on multi-temporal aerial photographs and satellite images;

(2) understand the extent to which changes in woody cover are explained by decadal changes in mean annual rainfall in southern African savannas;

(3) test the effect of a 15% reduction in rainfall on the growth of *Vachellia karroo* (*V. karroo*) saplings over a four year period at a savanna site in Zimbabwe;

(4) understand the interactive effects of rainfall and N availability as mediated by herbaceous competition on the growth of *V. karroo* saplings in semi-arid savannas, and

(5) model the potential effects of climate change on the spatial distribution of *V. karroo* species identified as key woody encroacher species in southern Africa.

1.6 Working Hypotheses

This thesis tests several hypotheses based on the observational, experimental and modelling approaches adopted in the study. Based on the intensity-dominant scale approach, we test the hypotheses that:

(1) the encroachment of woody patches into the surrounding grassland matrix causes a shift in the dominant scale. This shift in the dominant scale can be detected using a discrete wavelet transform regardless of whether aerial photography and satellite data are used;

(2) as the woody patch size stabilises, woody cover tends to increase thereby triggering changes in intensity

3) changes in the cover and spatial extent of woody patches induced by determinants of savanna ecosystem can be characterised using the intensity-dominant scale approach.

The experimental study tests the following hypotheses:

4) since tree growth is currently limited by rainfall, a 15% decrease will further constrain woody sapling growth.

5) as grasses are more efficient in utilising resources in the upper soil layer than woody species, N addition will stimulate growth of grass species at the expense of woody species thereby amplifying their suppressive effects on woody species.

6) N addition combined with rainfall reduction may dampen the competitive effects of grasses on woody species.

In modelling the habitat suitability of *V.karroo* under a future climate, we hypothesise that:

7) with the projected decreased in rainfall coupled with an increase in temperature, the suitable habitat of *V.karroo* will contract.

1.7 Study Area

The study was carried at six study sites (Nyanga:32^{o} 47.58' East and 18^{o} 18.30' South, Chivero:17°54′42″ South and 30°47′15″East, Kyle:20°11'20.01" South and 30°58'58.17" East), Ngezi:18° 40' 59.12" South and 30°24' 0.68" East, Matopos:20° 30´ South and 28° 30´ East, Tuli: 21° 58′ 13″ South and 29° 7′ 22″ East) located along a rainfall gradient in a southern African savanna. The rainfall gradient ranges from less than 400mm in western parts of the country to more than 1300 mm in eastern parts of the country. The field experiment was only performed at Kyle Game Reserve located in the southern parts of Zimbabwe. The remaining study sites were used in the testing the utility of the intensity-dominant scale framework in characterizing woody dynamics as well as determining the role of rainfall in explaining woody the dynamics based on historical data. Detailed descriptions of the study sites as well as the study approaches are described in the respective chapters.

1.8 Study species

The study tested the effects of rainfall suppression and nitrogen addition on the growth of *Vachellia karroo* species (formerly known as *Acacia karroo* Hayne), one key encroacher species in southern Africa. The species is in Leguminosae (Fabaceae) family and belongs to the *Mimosoidae* sub-family (Chirara, 2001). *V. karroo* nodulates more than other common southern African *Vachellias* and its growth are often associated with symbiotic associations with *Rhizobium* species (Barnes *et al.*1996). *Vachellia karroo* is a drought-resistant leguminous woody plant that is commonly referred to as Sweet thorn. The species is dominant and widespread across savannas of Africa and occurs in Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland and Zimbabwe. *V.karroo* grows in areas where rainfall ranges from as little as 95mm to as much as 1500mm. It is found at altitudes ranging from near sea level to around 800 to 1700m (Barnes et al., 1996). The species thrives well in areas with a mean annual temperature of between 12.4 ºC to about 24ºC. *V. karroo* is tolerant to all but the most severe frost in southern Africa Barnes et al., 1996). The species thrives in a variety of soils that include clay, alluvial clay-loam soils, shales, sand and even in highly acidic soils. Once established, the species is tolerant to drought and fire. *V karroo* prefers is one of the key browse species for livestock and wildlife especially during the dry season. This species is regarded as central to the persistence of savanna ecosystem function and stability (Sankaran et al., 2005, Scholes and Archer, 1997) as well as having economic importance to livelihoods of human communities in this ecosystem. However, the species can out-compete grasses in dry areas and may form mono stands that results in decrease in grass productivity (Kraaij and Ward, 2006).

1.9 Thesis outline

This thesis consists of seven chapters composed of a general introduction (Chapter 1) and a synthesis (Chapter 7) based on five stand-alone manuscripts (Chapters 2-6) that have either been published in or submitted to peer-reviewed international scientific journals. These chapters can be read independent of each other though they have a common thread that contributes to the understanding woody patch dynamics in semi-arid savannas. As these chapters were submitted for review independent of each other, some repetition especially in the description of methods and study sites is therefore unavoidable. The greater portion of the submitted or published manuscript has been retained resulting in overlaps among these chapters. However, these overlaps are considered insignificant given the easy of understanding offered by reading each paper as a standalone chapter.

The first chapter provides a general context to the study. The chapter explores key models that have been developed to explain the structure and structure of savanna ecosystems. The chapter ends by providing the objectives and hypotheses tested in the study including a brief description of the study sites.

The second chapter explores the utility of wavelets implemented within the intensity-dominant scale framework in characterizing woody encroachment. Woody encroachment can have profound effects on the ability of savanna ecosystems to provide goods and services to society (Sankaran et al., 2008). It is therefore crucial to understand the key drivers of woody encroachment in savannas. To this end, the third chapter tests whether decadal changes in mean annual rainfall could explain changes in woody patch dynamics at multiple savanna sites distributed across a gradient of increasing rainfall availability in Zimbabwe.

Although there are uncertainties regarding magnitude of precipitation decrease over southern Africa (IPCC, 2014a), it is currently not known how a decrease in precipitation would affect woody patch dynamics in semi-arid savannas. Therefore, chapter four experimentally tests the effects of a 15% rainfall decrease, a key savanna determinant, on the growth of *Vachellia karroo*. *V. karroo* is a nitrogen-fixer woody species that has been identified as one of the key encroacher species in southern African savannas.

In chapter five, the combined effects of precipitation decrease and N addition on the growth of *V. karroo* are assessed using a relatively long field experiment installed at Kyle Game Reserve, in southern Zimbabwe. Knowledge of the combined effects of these two resources is critical for savanna management in a changing world.

Climate change projections in southern Africa show a drier and a warmer future climate (IPCC, 2014a). It is not yet clear how these changes are going to affect the suitable habitat of woody encroacher woody species in southern African savannas. Chapter six explores the potential effects of climate change on the bioclimatically suitable habitat of *Vachellia karroo*.

Chapter seven provides a synthesis of the key findings presented in chapters two to six. In addition, the chapter highlights contribution of this thesis to the understanding of woody patch dynamics as influenced by key resources, that is, water and N. The chapter concludes by providing recommendations for future research that could further enhance our understanding of the key determinants of woody patch dynamics in savannas.

Chapter 2

Wavelet-based detection of woody encroachment in a savanna using multi-temporal aerial photographs and satellite imagery

This Chapter is based on:

Shekede, M.D., Murwira, A. and Masocha, M., 2015. Wavelet-based detection of bush encroachment in a savanna using multi-temporal aerial photographs and satellite imagery. *International Journal of Applied Earth Observation and Geoinformation, 35*, pp.209-216.

Abstract

Although increased woody plant abundance has been reported in tropical savannas worldwide, techniques for detecting the direction and magnitude of change are mostly based on visual interpretation of historical aerial photography or textural analysis of multi-temporal satellite images. These techniques are prone to human error and do not permit integration of remotely sensed data from diverse sources. Here, we integrate aerial photographs with high spatial resolution satellite imagery and use a discrete wavelet transform to objectively detect the dynamics in woody encroachment at two protected Zimbabwean savanna sites. Based on the recently introduced intensity-dominant scale approach, we test the hypotheses that: (1) the encroachment of woody patches into the surrounding grassland matrix causes a shift in the dominant scale. This shift in the dominant scale can be detected using a discrete wavelet transform regardless of whether aerial photography and satellite data are used; and (2) as the woody patch size stabilises, woody cover tends to increase thereby triggering changes in intensity. The results show that at the first site where tree patches were already established (Lake Chivero Game Reserve), between 1972 and 1984 the dominant scale of woody patches initially increased from 8 m before stabilising at 16 m and 32 m between 1984 and 2012 while the intensity fluctuated during the same period. In contrast, at the second site, which was formerly grass-dominated site (Kyle Game Reserve), we observed an unclear dominant scale (1972) which later becomes distinct in 1985, 1996 and 2012. Over the same period, the intensity increased. Our results imply that using our approach we can detect and quantify woody/bush patch dynamics in savanna landscapes.

2.1 Introduction

Savannas are ecosystems co-dominated by a continuous grass layer and scattered trees (Frost et al., 1985). Savannas account for a fifth of the terrestrial surface (Scholes and Archer, 1997b) and contribute up to 30 % to global net primary production (Grace et al., 2006). In addition, savannas support the largest diversity of mammals on Earth and constitute a major source of livelihood for more than half of the total human population in Africa through agriculture, grazing as well as fuelwood harvesting (Sankaran et al., 2005c, Scholes and Archer, 1997b). In this regard, knowledge on savanna ecosystems and their dynamics is important.

The ability of the savanna to provide services to society is dependent on the persistence of a stable mosaic of grasses and trees, which is now undergoing transformation due to widespread woody encroachment being experienced on a global scale (Wigley et al., 2009b). Woody encroachment is the gradual increase in woody plant species in previously grassland, tree-grass-dominated areas or tree-grass co-dominated ecosystems (Archer 1990, Archer 1994, Sankaran et al., 2004, Khavhagali and Bond, 2008, van Auken 2009). Woody encroachment is widely hypothesized to be driven by a combination of factors that range from overgrazing by domestic livestock to global ones that include elevated atmospheric CO_2 concentrations, increased nitrogen deposition and climate change (van Auken et al., 1985), Archer et al. 1995, Briggs et al. 2005, Wigley et al. 2009). The increase in woody species in savannas results in reduced rangeland carrying capacity for livestock and wildlife (Archer, 1994, Kraaij and Ward, 2006b, Rohner and Ward, 1997, Timberlake, 1994, Wiegand K, 2006). Thus, an understanding of the process of woody encroachment is important as a preamble to the development of methods for the detection and characterisation of the process.

As mentioned earlier, the development of methods that allow for the detection and characterisation of woody encroachment hinges upon the understanding of its progression in the first place. Archer (1995) provides a conceptual framework for understanding the progression of woody encroachment in savanna ecosystems which can conveniently be subdivided into 3 key stages, i.e. initiation, cluster development and coalescence of woody clusters. The initialisation of woody encroachment starts with the dispersal and invasion of woody species in a previously grass dominated landscape. Next, clusters develop around established individual woody plants as a result of facilitation through nucleation process enhanced by avifauna dispersal (Yarranton and Morrison 1974) and increased resource availability through trapping of nutrients under wood canopy (Schlesinger et al., 1990; Whitford, 1992). Finally, with further recruitment of woody species around the focal woody plant, there is enlargement of young and old clusters resulting in coalescing of discrete clusters (Archer 1995). However, we assert that the process of woody encroachment is a non-linear ecological process. For instance, drought years may result in the contraction of woody clusters and expansion of the herbaceous layer while years of above normal rainfall may result in enhanced recruitment of woody plants (Roques et al. 2001, Sankaran et al. 2005, Angassa and Oba 2007). Thus, the dynamics in these two life forms are influenced by recruitment of invading woody species in response to changes in rainfall regimes (Wiegand et al. 2006).

Traditionally, the study of woody encroachment involves the use of fieldwork and aerial photography. For the latter, studies have mainly used manual digitizing (Ansley et al., 2001) and grey-scale partitioning or level slicing (Lahav-Ginott et al., 2001) to detect woody encroachment in savanna ecosystems. While these methods have enabled the determination of tree or tree cluster location and size, they have often failed to determine the window size, i.e., the scale at which woody encroachment occurs, yet all ecological processes such as woody encroachment are intrinsically scale dependent (Wiegand et al., 2006, Wiens, 1989). Only recently, have ecologists started having interest in developing and applying methods that can objectively quantify the scale dependency of ecological processes. In that regard, variograms (He et al., 2006) and recently wavelets have been applied to the quantification of spatial scale of vegetation structure in forests (Bradshaw and Spies, 1992) and savanna (Strand et al., 2008, Strand et al., 2006). However, to date these studies have not been using any analytical framework that can simultaneously incorporate vegetation density or cover and linear dimension (scale). This has made it difficult to characterise vegetation dynamics in landscapes such as the savannas where ecological processes consist of a largely multi-scale structure. Recently, Murwira and Skidmore (2005) developed the intensity-dominant scale approach which may be able to simultaneously handle changes in cover and scale. However, to the best of our knowledge application of the intensity-dominant scale approach to understanding woody encroachment is still in its infancy.

The intensity-dominant framework is based on the premise that the distance between woody and grass patches in a savanna landscape can be objectively quantified using remotely sensed data based on their contrast in the image. For instance, consider a savanna landscape in which tree and grass patches are separated by various linear distances i.e., 200 m, 350 m and 515 m (Figure 2.1a). On a remotely sensed image, typically an aerial photograph or satellite image, the woody patches would appear as dark tones while the grass patches would appear as lighter tones (see Figure 2.1b). Based on this image, we can deduce the linear distances at which the maximum contrast in dark and lighter tones (representing woody and grass patches respectively) occur, i.e., 200 m, 350 m and 512 m. We refer to the most frequently occurring distance as the dominant scale while the extent of the difference in contrast is the intensity of the pattern or just intensity (Figure 2.1c). Overall, we can summarise this savanna landscape as having a dominant scale of 512 m, which is the distance at which woody and grass patches are interspersed. Thus, the dominant scale is predicted to correlate well with the spatial extent or dominant linear dimension of either woody or grass patches within the study sites while intensity coincides with the contrast in the density of woody and grass cover.

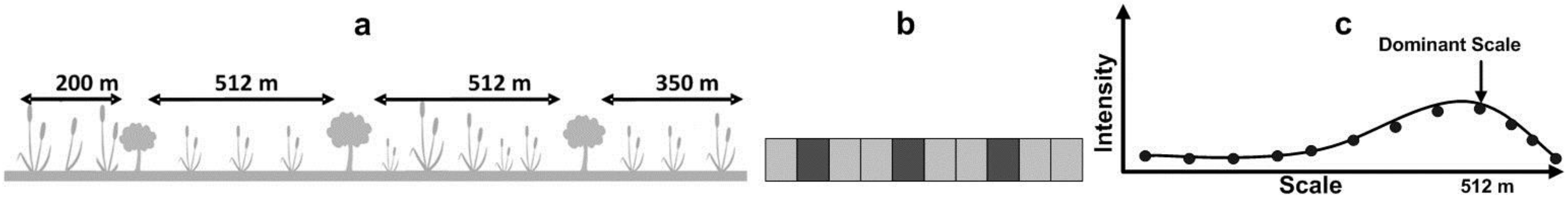

Figure 2.1: Conceptual framework showing the relationship between the dominant patch dimension in the landscape (a), the digital representation of woody plants and grasses in an aerial photograph or satellite image (b) and characterization of tree-grass structure from satellite image or aerial photograph using wavelet transform based on the intensity-dominant scale approach (c). Light grey pixels represent grass while dark grey indicate woody species.

In the context of woody encroachment, we envisage several predictions based on the intensity-dominant scale approach. Firstly, during the initiation phase of woody encroachment when woody clusters are few, we predict a large dominant scale that reflect the large size of the grassland and a low intensity as a result of low woody cover and grass cover contrast. Next, during the cluster development stage, we predict a decrease in the dominant scale due to increasing woody patch size resulting from further recruitment of woody plants. At this stage, intensity is expected to increase due to the increased contrast between grassland background and tree clusters. In fact, intensity is expected to be highest when the two life forms co-dominate. Finally, with further progression of woody encroachment coalescence and canopy closure, we predict that intensity decreases reflecting near homogeneity or dominance in woody cover. However, since woody encroachment is non-linear, we predict that both the dominant scale and intensity fluctuate between low and high. In this regard, it is reasonable to hypothesise that the intensity-dominant scale framework can be used to track tree and grass spatial dynamics resulting from woody encroachment in a savanna ecosystem. Like earlier-mentioned, although the intensity-dominant scale approach has been successfully used to characterise spatial heterogeneity in different landscapes (Murwira and Skidmore, 2005; Pittiglio et al., 2011), the issue of whether this method can be used to characterise the process of woody encroachment has not yet been tested.

In this study, we test whether the intensity-dominant scale approach implemented using a wavelet transform can be used to detect woody encroachment using historical aerial photographs and satellite images in two protected savanna landscapes in Zimbabwe. Specifically, based on the recently developed intensity-dominant scale approach, we test the hypotheses that: (1) the encroachment of woody patches into the surrounding grassland matrix causes a shift in the dominant scale. This shift in the dominant scale can be detected using a discrete wavelet transform regardless of whether aerial photography and satellite data are used; and (2) as the woody patch size stabilises, woody cover tends to increase thereby triggering changes in intensity. The quantification of tree-grass dynamics is a first step towards understanding the magnitude and direction of change as well as insights into the possible mechanisms that drive woody encroachment.

2.2 Materials and Methods

2.2.1 Study area

The study was conducted at two study sites, i.e., Lake Chivero game reserve located at latitude 17^{o} 55’ and longitude 30^{o} 48’ and Lake Kyle (Mutirikwi) game reserve located at 20^{o} 06’ of latitude and longitude 30^{o} 58’. These two sites were selected because they were established around the same time (Kyle 1961 and Chivero 1962) and have typically similar vegetation and herbivore species. Consumptive human activities are prohibited in game reserves, making the two study sites ideal for studying woody/woody encroachment and densification in a natural setting.

2.2.1.1 Lake Chivero Game Reserve

The game reserve was established in 1962 and occupies 1,867 hectares (Zimbabwe Parks and Wildlife Authority). An area covering 1.024km by 1.024km was selected within the game reserve for this study. Figure 2.2 shows the aerial photographs and GeoEye satellite images of the study site.

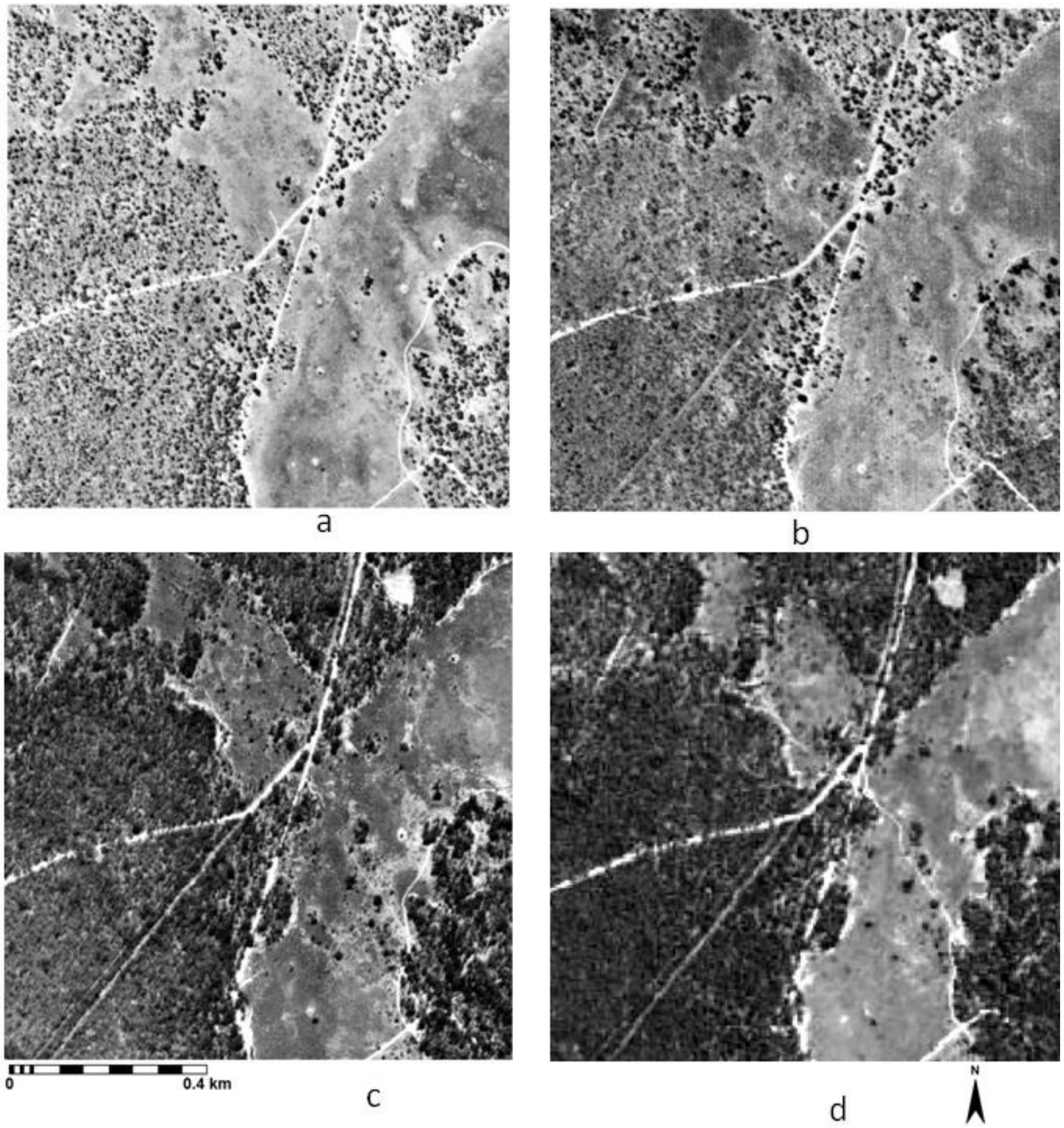

Figure 2.2: Aerial photographs for the years 1972 (a), 1984 (b), 1995 (c) and GeoEye satellite image for 2011(d) used for analysing woody encroachment at Chivero Game Reserve.

The mean annual rainfall at Lake Chivero Game Park is 829 mm (Zimbabwe Meteorological Services Department). The precipitation regime is highly variable in both space and time. The predominant vegetation in Lake Chivero Game Park is the miombo woodland (*Brachystegia* *spiciformis* and *Julbernada globiflora)* that is found in association with *Terminalia sericea, Parinari curatellifolia, Monotes glaber,* and *Burkea africana* (Malinga, 2001). The main herbivores found in the Game Park include; eland (*Taurotragus oryx*), giraffe (*Giraffa cameleopardalis*), kudu (*Tragelaphus strepsiceros*), tsessebe (*Damaliscus lunatus*), wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), white rhino (*Ceratotherium simum*), sable (*Hippotragus niger*), waterbuck (*Kobus ellipsipyrimnus*), reed buck (*Redunca arundinum*), impala (*Aepyceros melampus*), grey duiker (*Sylvicarpra grimmmia*) and common warthog (*Phacochoerus africana*).

2.2.1.2 Kyle Game Reserve

Kyle Game Reserve (KGR) was proclaimed a nature reserve in 1961 and covers an area of 44km^2. Within the reserve, a 1,024km by 1,024km site was selected for this study. Figure 2.3 shows the aerial photographs and GeoEye satellite images of the study site. The Reserve is situated midway between the Highveld and the lowveld ecological complex in Zimbabwe at an altitude of 1050 m above sea level. The surrounding area mainly consists of privately owned commercial farms in the north and south west while communal land predominates in the east. KGR receives a mean annual precipitation of638 mm (Zimbabwe Meteorological Services Department). Similar to Lake Chivero Game Reserve, the rainfall season in KGR is characterised by low and highly erratic rainfall. The dominant vegetation found in the Game Reserve is miombo (*Brachystegia/Julbernardia*) woodland in the north and south east.

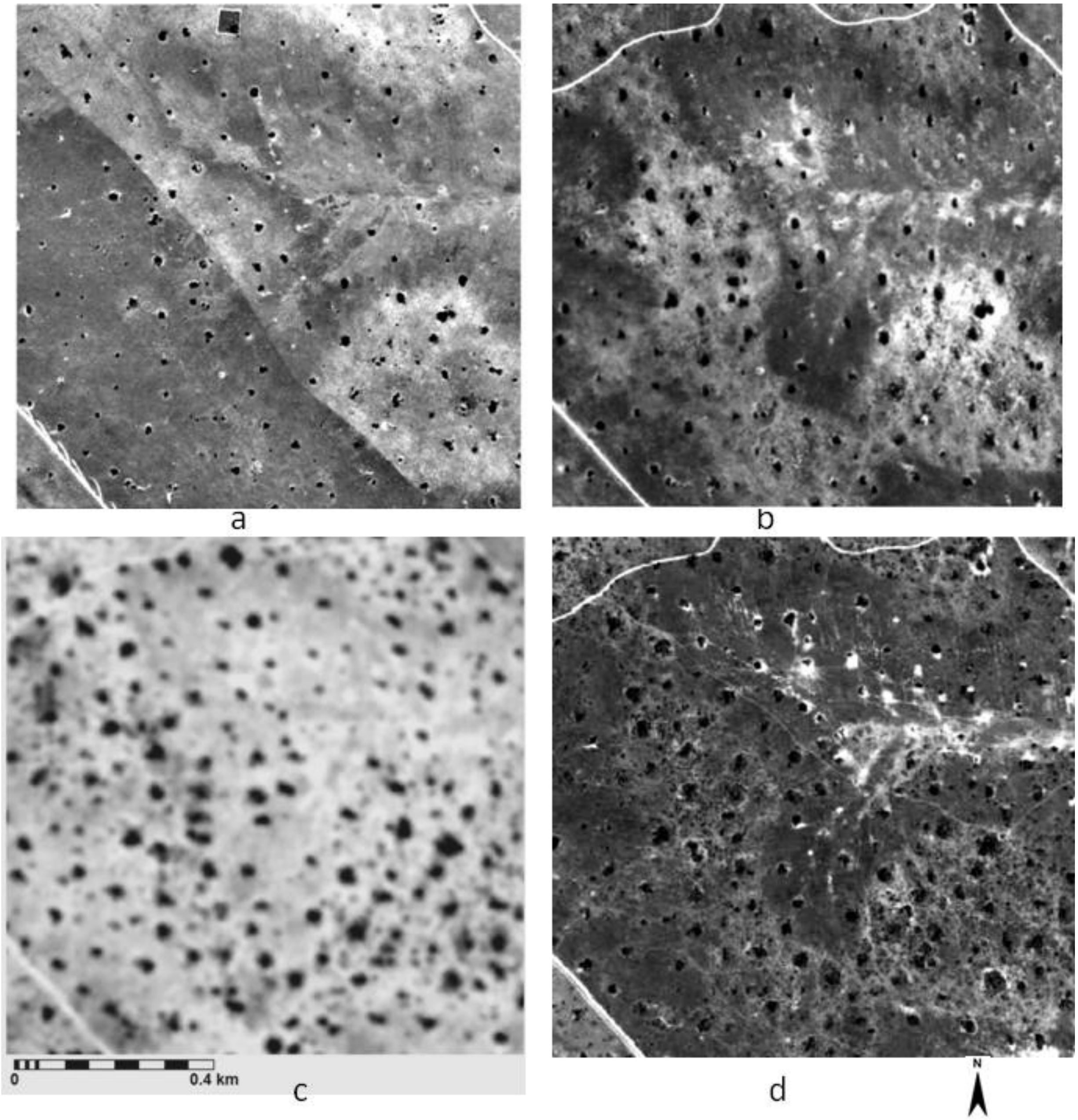

Figure 2.3: Aerial photographs for the years 1972 (a), 1984 (b), 1996 (c) and GeoEye satellite image for 2012 (d) used for analysing woody encroachment at Kyle Game Reserve.

Brachystegia spiciformis and *Julbernardia globiflora* dominate the woodland, whereas the woodyland is dominated by *Dodonaea viscosa*, *Dichrostachys cinerea*, and the invasive *Lantana camara* (Masocha and Skidmore, 2011). *Hyparrhenia filipendula* and *Hyperthelia dissoluta* (Vincent and Thomas, 1960) are the two grass species that are predominant in the open grassland areas of the reserve. The dominant wildlife found in the park includes warthog (*Phacochoerus africana*), buffalo (*Syncerus caffer*), white rhinoceros (*Ceratotherium simum*), impala (*Aepyceros melampus*), giraffe (*Giraffa cameleopardalis*), zebra (*Equus burchelli*), eland (*Taurotragus oryx*) kudu (*Tragelaphus strepsiceros*), buffalo (*Syncerus caffe)* and baboons (*Papio ursinus*).

2.2.2 Aerial photographs

We used dry season aerial photographs of 1972, 1984 and 1995 for Lake Chivero Game Reserve and 1972, 1985 and 1996 aerial photographs for Lake Kyle Game Reserve to detect and characterise woody encroachment in the savanna study sites of Zimbabwe (Table 2-1). Zimbabwe is characterised by a distinct wet and dry season. The wet season begins in late November and terminates in March while the dry season begins in April and ends at the end of October and early November (Kuri et al., 2014). Since all the aerial photographs were acquired during the dry season, we considered as insignificant the effects of radiometric differences due to phenology and sun angle for the purposes of our study (Pittiglio et al., 2011, 2013). In fact, the intensity-dominant scale approach used in this study is robust in the detection of the dominant scale even when using images acquired on different dates (Pittiglio et al., 2011, 2013).

Table 2-1: Date of acquisition of aerial photographs used for assessment of woody encroachment in the two study sites located in Zimbabwe

Study Site	Date of Acquisition
Chivero Game Park	9 September 1972 4 September 1984 14 June1995
Kyle Game Reserve	11 August 1973 13 June 1985 28 August 1996

The aerial photographs were available at a scale of 1:20,000.These historical aerial photographs were selected because they provide a large temporal window (>30 years) and a fine spatial scale allowing for the determination of long-term changes in tree-grass dynamics. This would not be possible with satellite data since there was no high spatial resolution capacity from satellite remotely sensed data in the 1970s. Specifically, a period of ~39 years used in this study is deemed long enough to observe changes in tree-grass ratios in the study sites following (Pickett, 1982). All the aerial photographs were acquired from the Surveyor General Department of Zimbabwe in Harare.

In order to prepare the photographs for woody encroachment analysis, we first scanned the aerial photos using a ColorTracSmart LF Ci40 scanner at a resolution of 1200 dots per inch (dpi) and imported them in ILWIS GIS (ITC, 2002). We then performed inner orientation, i.e., referencing the four fiducial marks on the scanned aerial photograph based on the camera focal length, principal distance and scale information readily avail-able on the aerial photographs. This procedure establishes the geometric relationship between the aerial photograph coordinate system and the instrument coordinate system. Following the registration of fiducial marks, we used an orthorectified the aerial photographs with the aid of scanned and georeferenced 1:50:000 topographic maps and the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) 30 m Digital Elevation Model as the elevation source. The aerial photographs were orthorectified based on the Universal Transverse Mercator Projection Zone 36 using Modified Clarke 1880 Spheroid. Ground Control Points used for orthorectification were obtained by identifying features such as road intersections and fence corners visible in both the geo-referenced topographic maps and the aerial photographs. Finally, we resampled the orthorectified aerial photographs for the respective study sites to the same geo-reference to ensure comparability and for north orienting the photos. The accuracy of the orthorectification was assessed using the root mean square error (RMSE) and was less than 0.5 m for all the aerial photographs.

2.2.3 Satellite images

In Zimbabwe, formal aerial surveys were carried up to 1996 after which there are no aerial photographs covering the study area. To this end, we used the June 2011 and November 2012 GeoEye satellite images for Lake Chivero and Kyle Game Reserve respectively, made available in Bing (www.bing.com). GeoEye satellite imagery had a nominal spatial resolution of 1.64m which had minimal effect on our analysis following Pittiglio *et al*, (2011) who demonstrated that wavelets can detect the same dominant scale using images with different initial spatial resolutions provided the dominant scale in the landscape is magnitudes greater than all the initial pixel sizes. In order to make GeoEye data compatible with aerial photographs, we converted it to 8-bit greyscale using the colour separation algorithm in ILWIS GIS (ITC, 2005). We also resampled the grey scale images for the respective study sites to the same spatial resolution as aerial photographs.

2.2.4 Wavelet Transform

We performed a wavelet transform based on a Haar wavelet (Bruce and Gao, 1996) to detect woody encroachment and intensification in Chivero and Kyle game reserve study sites. A Haar wavelet was selected because of its ability to detect edges that are essential for the delineation of woody patches in the study site as well as its efficiency in handling digital imagery. Wavelet transform involves the convolution of two functions, i.e., the smooth function $\varphi(x, y)$ and detail function $\phi(x, y)$ with a data function $f(x, y)$ at successive bases, (2^j), i.e., $j = 0, 1, 2, 3 \ldots J$ in the vertical (north-south), diagonal (northeast-southwest and southeast-northwest) and horizontal (east-west) directions (Murwira and Skidmore 2005). As a result, a wavelet transform yields a set of scale (i.e., *j* = 0, 1, 2, 3… *J)*, direction and location specific coefficients. Higher coefficients are obtained at a scale level j where there is a match between the wavelet and the data function while lower coefficients are realized when wavelet does not coincide with the curve of the function.

As a preamble to performing a wavelet transform, we denoted the 1970s, 1980s and 1990s aerial photographs by *(F(x, y), W(x,y)* and *Z(x,y)* respectively. To this end, we performed a Haar wavelet transform for each of the three aerial photographs as follows:

$$\hat{F}(x,y) = S_J(x,y) + \sum_{j=1}^{J} \sum_{dir} D_j^{dir}(x,y)$$

Equation 1

$$\hat{W}(x,y) = S_J(x,y) + \sum_{j=1}^{J} \sum_{dir} D_j^{dir}(x,y)$$

Equation 2

$$\hat{Z}(x,y) = S_J(x,y) + \sum_{j=1}^{J} \sum_{dir} D_j^{dir}(x,y)$$

Equation 3

Where $\hat{F}(x, y)$, $\hat{W}(x, y)$ and $\hat{Z}(x, y)$ are the wavelet approximations for the 1970s, 1980s and 1990s aerial photographs respectively. S_J represents the smooth coefficients and D_j^{dir} are the directional detail coefficients. We performed the same wavelet transform on the 2011 and 2012 GeoEye satellite images of Chivero and Kyle study sites respectively. Wavelets are treated in greater mathematical detail elsewhere (Mallat, 1989).

All the aerial photographs were resampled to a grain (spatial resolution) of 2 m to enable 1) comparability of wavelet coefficients across the images and over the years and 2) to optimize computing space, as a resolution of 0.5 m would not give us any significant extra information because woody patches are normally magnitudes higher than 0.5 m. To this end, the smallest scale of wavelet analysis corresponds to the grain of the aerial photograph which was 2 m in this study. We selected the maximum scale level, J of 8 which equals to a spatial dimension of 256m based on our preliminary analysis which showed that there was no significant additional information that was gained from increasing the window size after the 256 window.

2.2.5 Calculating wavelet energy

Based on the wavelet coefficients derived from the wavelet transform, we calculated wavelet energy by dividing the sum of squares of the coefficients at base 2^j by the sum of the squares of all the coefficients in the wavelet approximations in $\hat{F}(x, y)$, $\hat{W}(x, y)$ and $\hat{Z}(x, y)$ (Murwira and Skidmore, 2005b). Energy at each of the scales was calculated as:

$$E_j^d = \frac{1}{E} \sum_{k=1}^{\frac{n}{2^j}} d^2 j(x, y), \ j = 1, 2, 3 \ldots\ldots J$$

Equation 4

Where $d^{j(x, y)}$ represents the detail wavelet coefficients at *j* and position *(x, y)*

E is the total sum of squares of $\hat{F}(x, y)$ or all squared coefficients and $n/2^J$ denotes the number of coefficients at level *j*. Following the same procedure, we calculated the wavelet energy for the 2011 and 2012 GeoEye Satellite images for Kyle and Chivero Game Reserves, respectively.

The calculations in equation 4 result in wavelet energy i.e. normalized coefficients at each scale level *j* for each of the aerial photographs and satellite image.

2.2.6 Determination of dominant scale and intensity

To determine the dominant scale and intensity, we plotted the wavelet energy values as a function of scale for each of the aerial photographs. From the wavelet energy curves, we determined the intensity and the dominant scale through noting the local maxima in the energy value of the curve and the corresponding scale values. In other words, maximum wavelet energy value represents the intensity while the dominant scale is the scale size at which this maximum energy is realized. The wavelet transforms were implemented in S-PLUS Version 8 (TIBCO Software Inc).

2.3 Results

2.3.1 Changes in intensity and dominant scale of woody patches in Lake Chivero Recreational Park

Figure 2.4 illustrates results of discrete wavelet transform performed on the 1972, 1984 and 1995 aerial photographs and the 2011 GeoEye satellite image for Chivero. We observe that in 1972 the dominant scale, which corresponds with the average size of woody patches in a given year, was 8 m. It doubled to 16 m in 1984 and remained the same for 1995 before doubling again to 32 m by 2011. During the same period, the maximum variance exhibited by woody patches (i.e., their intensity), intially decreased by 14.8% between 1972 and 1984 before recording a four-fold increase between 1984 and 1995. A further 120% increase in the intensity occurred between 1995 and 2011. Overall, the dominant scale of woody patches quadrupled over the 39-year period while the intensity decreased slightly by 0.7%.

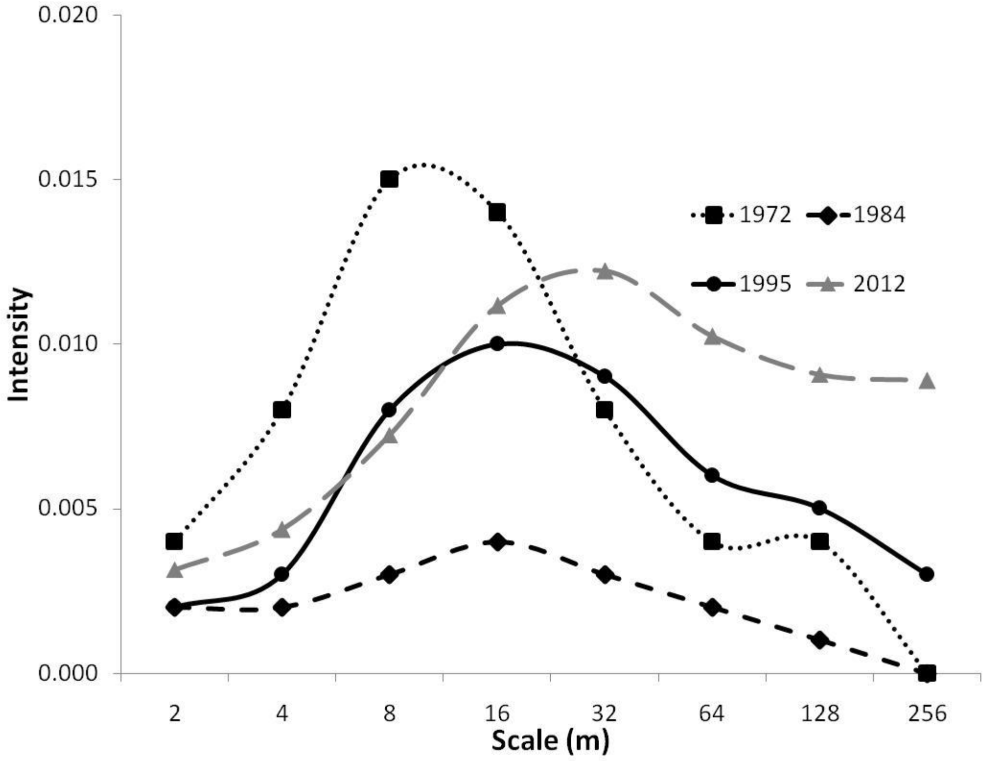

Figure 2.4: Changes in maximum intensity and dominant scale for the years 1972, 1984,1995 and 2011 at Chivero Game Reserve.

2.3.2 Changes in intensity and dominant scale of woody patches in Kyle Game Reserve

Figure 2.5 shows changes in the intensity and dominant scale for Kyle Game Reserve between 1972 and 2012. Initially, the dominant scale was not detected based on the 1972 aerial photograph but it equalled 32m in 1985 and remained the same for 1996 before decreasing to 16m by 2012. Although the dominant scale was the same for 1985 and 1996, we observed an 8-fold increase in intensity between the two years. Subsequent increases in intensity were recorded for the period between 1996 and 2012.

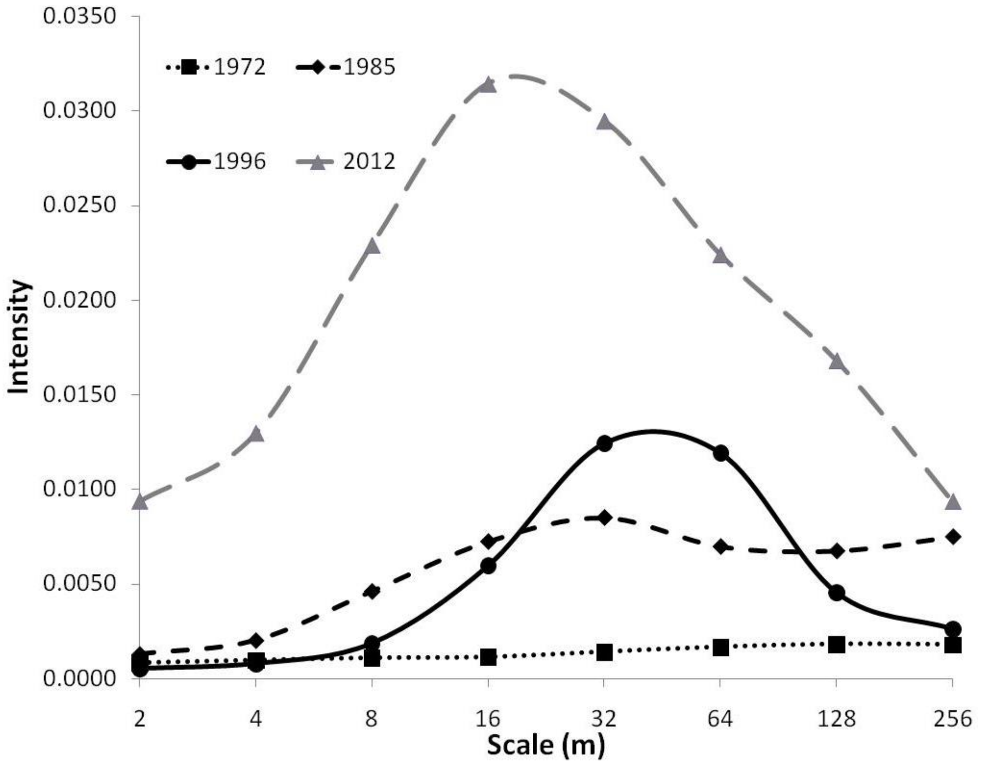

Figure 2.5: Changes in maximum intensity and dominant scale for the years of 1972, 1985, 1996 and 2012 at Kyle Game Reserve.

2.4 Discussion

Our results indicate that we can successfully detect and quantify the spatial dynamics of woody encroachment using a discrete wavelet transform applied on remotely sensed data based on changes in the intensity-dominant scale framework. Previously, the intensity-dominant scale concept was applied on Landsat-TM derived vegetation cover following wavelet transform to detect medium to large spatial scale (≥30m) changes in spatial heterogeneity in a savanna landscape in Zimbabwe following agricultural intensification between the 1980s and the 1990s (Murwira and Skidmore (2005b). However, our study used 2m spatial resolution aerial photographs which enabled us to detect fine spatial scale (≥ 2 m) woody encroachment in the two savanna study sites. In fact, all changes in woody patch size detected in this study were between 8 m and 32 m which would have been impossible using sensors such as MODIS and Landsat TM.

The most important insight into woody encroachment gained by using the wavelet transform within the intensity-dominant scale approach is that while the dominant scale (i.e., the average patch size) can remain the same, the intensity can change. For example, the increase in the intensity could be interpreted as indicative of thickening of woody patches which increases the degree of contrast or spatial heterogeneity in a landscape. In contrast, no changes in the dominant scale observed at our two savanna sites in some year simply that the encroachment of woody patches into the grassland matrix would have stabilised. These dynamics would have been difficult to detect using available techniques such as visual interpretation of aerial photographs, or textural analysis of multi-temporal imagery or post-classification comparison of time-series satellite data. Overall, the observed increases in the dominant scale at the humid savanna site (Lake Chivero Game Reserve) is consistent with the observation that woody encroachment in savannas results in increased woody patch size (Khavhagali and Bond, 2008). However, the results for the dry savanna site (Kyle Game Reserve) where the dominant scale decreased from 32 m to 16 m over a 39-year period imply that generalising the results of one site may be risky.

Moreover, results suggest that grasslands that are not colonised by woody patches exhibit low levels of spatial heterogeneity on panchromatic aerial photographs. This can be deduced from our failure to detect a distinct dominant scale at Kyle Game Reserve in 1972 following a wavelet transform. We however caution that on-detection of fine dominant scales within the grassland matrix maybe, in our case, an artefact of the panchromatic aerial photographs which have low spectral and radiometric resolutions and therefore a low capability to detect fine-scale tonal differences, which reflect the degree of contrast in a landscape. In fact, if high spectral and radiometric resolution remotely sensed data are used, fine dominant scales reflecting variations in grass biomass could be detected even in grass-dominated landscapes as reported in the literature. For example, He *et al*, (2006) used fine spatial resolution imagery to detect fine scale spatial variations in grassland and detected cyclic patterns of grassland as well as locations where high variations were present.

Results of this study indicate that when trees and grasses co-dominate the detected dominant scales are more defined ordistinct. This suggests that a grassland that is increasingly being encroached by woodlands is characterised by increasing detectability of distinct dominant scales reflecting increasing levels of contrast in the landscape resulting from woody encroachment. Although it is not surprising that landscapes with low spatial heterogeneity such as grasslands do not exhibit distinct dominant scales (Figure 2.4) and that these only emerge at fine spatial scales before increasing with increasing sizes of woody patches,we assert that this finding may amplify the utility of the intensity-dominant scale framework in understanding tree-grass dynamics in savannas. Our results are therefore consistent with observations of Pittiglio *et al*, (2011) who, although assessing the utility of waveletes in detecting fragmentation, found that the dominant scale changed with levels of fragmentation in a savanna landscape due to agricultural expansion. Overall, our results suggest that by using wavelets to characterise dominant scales, we cannot only charactersie woody encroachment at various spatial scales but we also gain understanding of whether expansion of woody patches, their shrinking or stabilisation may be coincident with thickening. Although it appears counter-intuitive that the dominant scale at which the woody patches express themselves in a landscape may increase while intensity decreases as observed in Chivero, we assert that this makes ecological sense as it implies that due to ageing, die-back of individuals recruited in the same year may occur resulting in the thinning of the patch.

The findings of this study indicate that intensity applied within the intensity-dominant scale framework is a useful tool for detecting changes in the density of woody cover in woodland patches over time even when using images acquired at different times. For example, at Kyle Game Reserve, the intensity increased in some years reflecting increases in woody cover while the dominant scale remained constant. In contrast, in Chivero, woodland patch size initially increased between 1972 and 1984 but stabilised between1984 and 2011 while intensity initially decreased from a high in1972 to a low in 1984 and an intermediate level in 2011. To this end, we deduce that changes in intensity provide a basis for measuring increasing densification within woody patches following woody encroachment. Our results are confirmed by Bradshaw and Spies (1992) who observed differences in intensity as a function of canopy cover and stand age. Specifically, Bradshaw and Spies (1992) found that young stands with dense, continuous and uniform canopies have low intensity (less contrast) across all spatial scales. Although not explicitly tested in this study, a previous study has shown a close correlation between variation in reflectance and spectral indices (proxies for intensity) and plant species diversity (Mutowo and Murwira, 2012). We thus assert that the intensity-dominant scale approach provides a robust method of characterising woody encroachment that can be implemented on images of different radiometric and spatial resolution as long as the spatial scale of the process is greater than the pixel size. In that regard, the method used here overcomes both the problem of cross comparison of images acquired at different times given that intensity is a normalised measure of contrast in dominant landscape features such as grass and woody mosaics as well as of different spatial and radiometric resolution.

Overall, the results from this study show that the dominant scale may stabilise after either an initial decrease (Kyle Game Reserve) or increase (Chivero Game Park) depending on the existing woodland-grassland ratios in the base year. We speculate that the stabilisation of the dominant scale observed at the two study sites in some years point toward the existence of multiple stable states as documented elsewhere (Baudena et al., 2010, Langevelde et al., 2003). Although the period of study we adopted might not be long enough to permit one to be conclusive on the existence of such multiple stable states, we assert that a period of ≥30 years could be long enough for such a state to be attained (Pickett 1982). Observations elsewhere show that a mosaic of small patches of trees in savannas be can persistent over time (Rietkerk et al., 2004) as a result of ecological buffering mechanisms such as fire and herbivory which causes mortality of woody seedlings and keeps the expansion of woody patches under check (Jeltsch et al., 2000a). It is therefore apparent from the findings of this study that the dominant scale and intensity approach when implemented with wavelets is able to capture the tree-grass dynamics in savannas in a repeatable and objective way thus contributing to increased understanding of tree-grass interactions at different stages of woody encroachment. However, we caution that the aerial photographs and satellite images used in the study span only four decades and the dominant scales detected are within the limits of the spatial extent of the study area we selected, as well as the characteristics of the multi-temporal datasets used.

What makes this study different from previous studies is on the application of the discrete wavelet transform on panchromatic aerial photographs and satellite images within the dominant scale-intensity framework for purposes of understanding wood-land encroachment and densification over time. Previous studies have either used manual digitising digital image classification (Moleele, 2002), or texture analysis (Ansley et al., 2001, Hudak and Wessman, 2001). Although 2-d spatial wavelet analysis was used to assess woody encroachment in savanna ecosystem before (Strand, 2006), this was not conducted within an intensity-dominant scale framework. It is only recently that Pittiglio et al. (2011) used the intensity-dominant scale approach but they used it to characterise woodland fragmentation. We thus assert that the dominant scale and intensity approach could also provide an objective and repeatable method of quantifying woody encroachment. However, we have to caution that aerial photographs have low radiometric and spectral information which maybe inadequate for use in inferring small scale biomass/cover variations from tonal differences. Thus, future studies could apply this approach on satellite images with high spatial and spectral resolution in order to improve our understanding of woody encroachment in savanna ecosystems.

2.5 Conclusion

In this study, we tested whether the emergence and densification of woody cover patches in protected savanna landscape where overgrazing by domestic stock is not a factor triggering encroachment can successfully be quantified using the dominant scale intensity approach. We conclude that using the intensity-dominant scale approach, we could quantify woody encroachment in savanna landscapes. We also conclude that woody encroachment can be detected based on the increasing contrast between grass and trees reflected in the intensity and dominant scale as a result of woody encroachment. Although we demonstrated the utility of wavelets implemented within the intensity-dominant scale framework in characterising woody encroachment, we did not test the extent to which rainfall explains woody patch dynamics. Thus, future studies could explore the extent to which changes in rainfall, could explain woody patchy dynamics in savannas.

Chapter 3

Decadal changes in mean annual rainfall drive long-term changes in woody-encroached southern African savannas

This Chapter is based on:

Shekede, M.D., Murwira, A., Masocha, M. and Zengeya, F.M., 2016. Decadal changes in mean annual rainfall drive long-term changes in bush-encroached southern African savannas. *Austral Ecology*, *41*(6), pp.690-700.

Abstract

Woody encroachment can have profound effects on the ability of savanna ecosystems to provide goods and services to society. It is therefore crucial to understand the key drivers of woody encroachment in savannas. In this study, we test whether decadal changes in mean annual rainfall significantly explain changes in dominant patch size as well as the density of woody patches at six protected savanna sites located along a rainfall gradient in Zimbabwe. We first performed Maximal Overlap Discrete Wavelet transform within the intensity-dominant scale theoretical framework on multi-temporal aerial photograph and high spatial resolution satellite imagery to objectively detect changes in the dominant patch dimension as well as the intensity of woody cover over a 40-year period at six test sites. We then pooled the data and performed regression analysis relating changes in dominant scale and intensity to decadal changes in mean annual rainfall in order to deduce a possible connection between dynamics of woody encroachment and rainfall variability. Our results indicate a significant nonlinear relationship between changes in the dominant scale and decadal changes in mean annual rainfall ($R^2 = 0.85$, $F_{13} = 35.96$, $P < 0.01$). In contrast, the relationship between decadal changes in mean annual rainfall and changes in intensity was weak and insignificant ($R^2 = 0.29$, $F_{13} = 2.69$, $P = 0.106$). These results imply the importance of annual rainfall in explaining long term changes in the dominant scale of woody patches. However, mechanisms other than rainfall likely explain changes in the intensity of woody cover and this needs further investigation.

3.1 Introduction

Savannas are unique ecosystems characterised by the co-existence of a continuous herb layer and a discontinuous woody layer (Scholes and Archer, 1997). They are central to human welfare and biodiversity conservation. For example, in Africa alone, tropical savannas support most of the continent's large mammalian herbivores including the African elephant (*Loxodonta africana*) (Scholes and Archer, 1997). Approximately 400 million people earn a living from goods and services provided by savanna ecosystems such as forage for livestock (Mistry, 2000). It is therefore reasonable to hypothesise that any process that alters tree-grass ratio in savannas particularly encroachment by woody plants, hereinafter, woody encroachment is likely to change ecosystem functioning. We thus assert that an understanding of the drivers of woody encroachment is key in setting management priorities for savannas so that they continue to support livelihoods and biodiversity.

Woody encroachment is a worldwide ecological phenomenon (Archer et al., 1988, Eldridge et al., 2011, Fensham et al., 2005.) that has also been observed in Africa (O 'Connor and Chamane, 2012). The socio-economic and ecological consequences of woody encroachment are many and on the balance of evidence most of these are negative. For instance woody encroachment is known to reduce rangeland productivity (Britz and Ward, 2007), reduce plant species diversity (Price and Morgan, 2008), and alter litter decomposition rates as well as nutrient recycling (Eldridge et al., 2013). Despite the extensive coverage of woody encroachment in literature, the mechanisms driving this ecological process are the least understood (Ward, 2005). Given the varied nature of the drivers of woody encroachment, several mechanisms have been proposed to explain this wide spread ecological phenomenon.

The proposed mechanisms include heavy grazing (Wigley et al., 2010.), climate variability (Sankaran et al., 2008), changes in fire frequency (O’connor, 1995), global warming (Van Auken, 2009), carbon fertilization (Buitenwerf et al., 2012) and global nitrogen deposition . A recent mechanism used to explain woody encroachment across southern Africa savannas is the extermination of mega-herbivores such as elephants and their subsequent absence in many small reserves (O'Connor et al., 2014a). What is most interesting is that while in some environmental settings it is the interaction among these factors that is crucial, none of these factors has been found to be universally applicable (Ineichen, 2014). This situation is further complicated by spatial autocorrelation that exists among the proposed drivers of woody encroachment (Hernandez-Stefanoni et al., 2011). In this regard, it is critical that further research into the ecological factors driving woody encroachment be conducted.

Among several factors that drive woody encroachment in savanna landscapes, rainfall is hypothesised to be the most important. This is because savannas are by nature water-limited ecosystems (Angassa and Oba, 2007). The massive woody species recruitment observed in years of above-normal and an equally massive woody species mortality experienced during drought years demonstrates the sensitivity of savannas to rainfall fluctuations (Twidel et al., 20114). Rainfall intensity and seasonal timing also constrain the extent to which maximum potential woody cover is realised. Specifically, low intensity rainfall regimes that percolate deep into the soil are likely to favour woody species at the expense of grasses (Kumaltiski and Beard, 2013). Moreover, a positive relationship between mean annual rainfall and woody cover has been reported in arid and semi-arid savannas of Africa (Sankaran et al., 2005). However, we assert that the universality of this relationship depends on the objectivity of the method used to detect woody encroachment in the first instance. For example, most approaches to detecting woody encroachment are based on visual interpretation of aerial photography or textural analysis of multi-temporal satellite images, which are often prone to human error. Recently, wavelet analysis has been proposed as an objective method of characterising woody encroachment. For example, Shekede et al., (2015) (Chapter 2) used a wavelet analysis to detect the dynamics of woody encroachment at two savanna sites in Zimbabwe based on the intensity-dominant scale framework (Murwira and Skidmore, 2005). However, the study did not test for the factors driving the dominant scale and intensity of woody cover in the study sites.

In this study we tested whether and to what extent the changes in the dominant scale and intensity of woody encroachment based on remotely sensed data are explained by decadal changes in mean annual rainfall over a 40-year period. We based our analysis on six protected savannas sites located along a rainfall gradient in Zimbabwe.

3.2 Conceptual Framework

Based on the intensity-dominant scale framework presented in Chapter two (Figure 2-1), we further illustrate the effect of rainfall on woody encroachment in a savanna landscape (Figure 3.1). First, consider a low rainfall site (<350 mm) in a semi-arid savanna landscape in which trees and grasses exist as alternating patches (Figure 3.1, S1). With low precipitation, woody cover is typically low due to insufficient moisture for massive woody species recruitment and thus the landscape is dominated by grass patches (Figure 1, S1). When one quantifies the structure of this landscape using the intensity-dominant scale framework, it is observed that the dominant scale is 512 m, capturing the dominant grass patches in both the landscape (a) and the image (b). However, since the grass patches are dominant in the landscape there is low intensity (c). Next, consider an intermediate rainfall site (>350 < 650 mm) in which trees and grasses co-dominate in the landscape (Figure 3.1, S2). In this case water is less limiting resulting in increased recruitment of woody species compared with the drier site. This in turn reduces the dominant scale to 256 m while there is a relative increase in the intensity. Finally, consider another savanna landscape which is wetter with mean annual rainfall greater than 650 mm (Figure 3.1, S3). In this savanna landscape, rainfall is sufficient to allow woody canopy closure in the absence of disturbances such as fire and herbivory (Sankaran et al., 2005b) and the dominant scale is at 350 m capturing the dominant woody patches while intensity is low due to dominance of woody patches in the landscape.

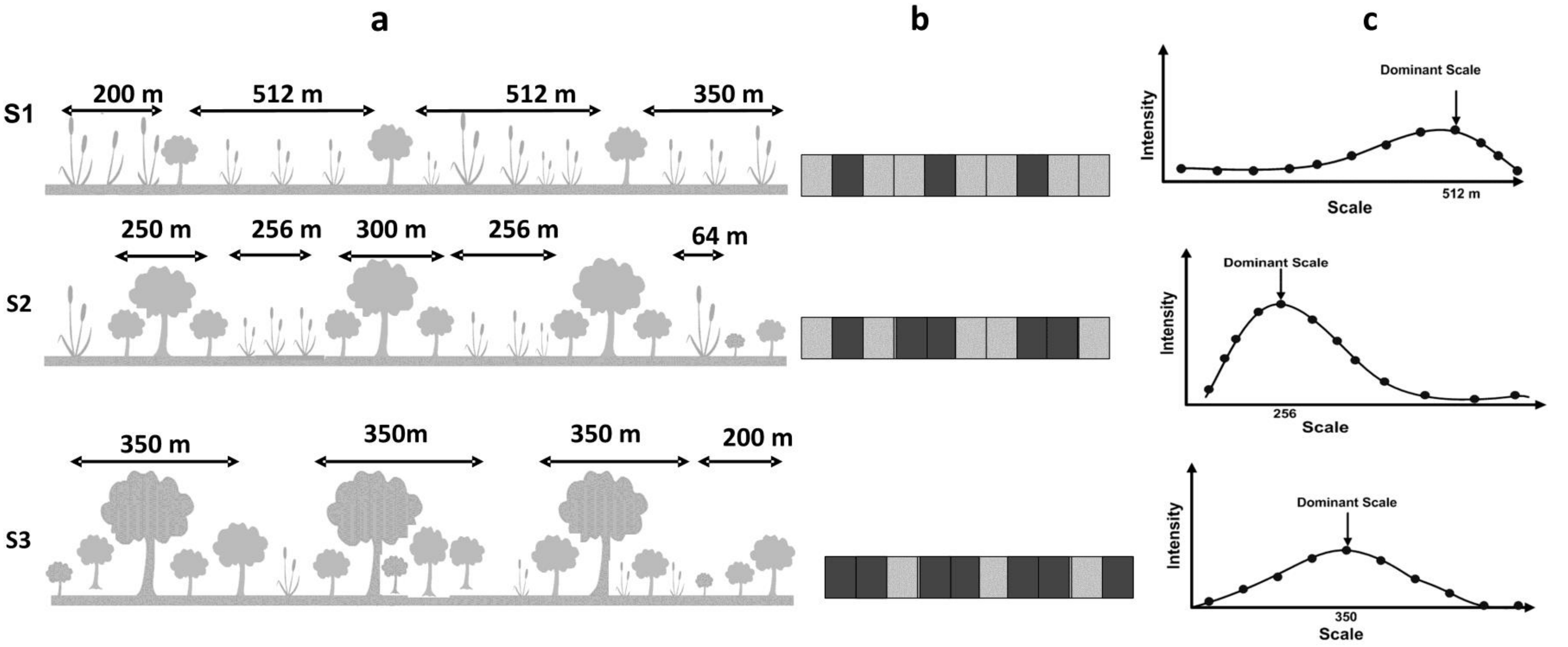

Figure 3.1: Conceptual framework showing the relationship between the dominant patch dimension in the landscape (a), the digital representation of woody plants and grasses in an aerial photograph or satellite image (b) and 3) characterization of tree-grass structure from satellite image or aerial photograph using wavelet transform based on the intensity-dominant scale approach. Light grey pixels represent grass while dark grey indicate woody species. S1, S2 and S3 represent low rainfall, intermediate rainfall and high rainfall sites, respectively.

It can therefore be deduced that rainfall has differential impacts on tree-grass matrix in savannas located along a gradient of rainfall. For instance at low rainfall site woody species recruitment and growth are limited by moisture availability leading to the dominance of grass since grasses are more efficient at using water than woody species. In this landscape, the dominant scale captures the large grass patches interspersed with scattered trees. Intensity is relatively low indicating the near homogeneous grass patches. With increasing rainfall, intensity may increase as more woody species are recruited in the grassland. Intensity, will remain relatively low as long as grass patches still dominate the landscape. However, at an intermediate rainfall site woody species recruitment is less limited by moisture compared to the low rainfall site and this is likely to trigger an increase in woody cover. In such a landscape trees and grasses co-dominate. In contrast, at the high rainfall site, woody species recruitment is not limited by moisture hence over time woody patches may coalesce due to increased opportunities for massive recruitment and low mortality. Without disturbances such as fire and herbivory this site can easily transit into woodland. Thus in such a landscape, a larger dominant scale compared to that of the intermediate rainfall site is expected.

Based on the fact that savanna structure is determined by moisture and nutrient availability as moderated by herbivory and fire (Sankaran et al., 2008, Scholes and Archer, 1997a), we would expect the dominant scale to, in some instances, vary independent of rainfall. For instance, frequent and intense fires reduce woody cover through limiting woody plant recruitment and in extreme cases induce mass mortality of juvenile and adult trees (Aisling et al., 2015). The suppressive effects of fires on woody species are also a function of rainfall, with the effects expected to be more at mesic sites than drier site due to higher fuel load. Similarly, mega herbivores such as elephants can reduce woody cover. We therefore hypothesise that changes in the cover and spatial extent of woody patches induced by determinants of savanna ecosystem can be characterised using the intensity-dominant scale approach.

3.3 Materials and Methods

3.3.1 Study sites

The study was based on six protected areas in the savanna landscapes of Zimbabwe following a rainfall gradient, i.e., one humid site, three intermediate rainfall sites and two low rainfall sites (Figure 3.2). The number of sites for each rainfall gradient was variable due to the non-availability of aerial photographs spanning a period of over 40 years.

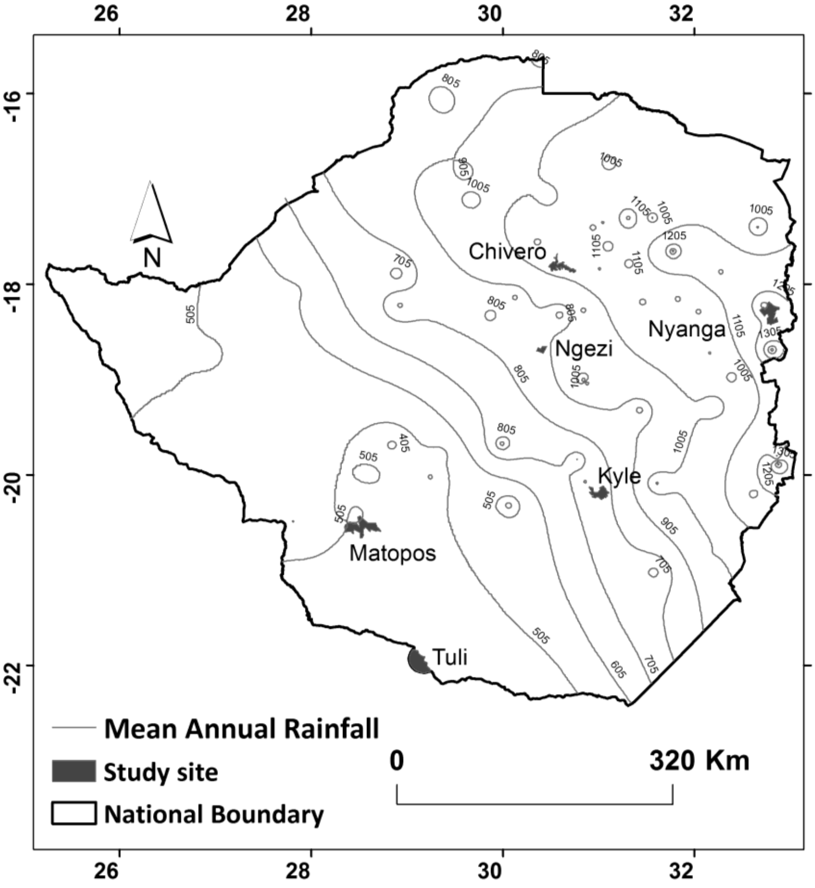

Figure 3.2 Location of the six study areas; Tuli, Matopos, Kyle, Ngezi, Chivero and Nyanga within Zimbabwe, overlain by rainfall isohyets. Isohyets are overlaid to indicate a gradient of decreasing rainfall in the country. The map units are latitude and longitude based on the WGS 1984 spheroid.

We chose protected areas in order to minimise the effects of other drivers of woody encroachment such as overgrazing by livestock. We also selected protected areas to control for human-induced disturbances that characterise savannas, such as agricultural expansion. We located the test sites along a rainfall gradient to enable us to test whether and by what magnitude rainfall influences woody encroachment in savanna landscapes with different rainfall regimes. We describe each of the study sites in relation to the rainfall gradient in the following sections.

3.3.1.1 Humid site

3.3.1.2 Nyanga National Park

Nyanga National Park was established in 1926 making it one of the oldest protected areas in Zimbabwe. The park is located at 32° 47.58' East and 18° 18.30' South and covers approximately 47,000 hectares (ha). Altitude ranges from 700 m to 2,592 m (ZPWMA, 2011). The park has a mean summer temperature of 26 °C and winter temperatures average -3 °C. Annual rainfall ranges from 1,500 to 3,500 mm (Zisadza-Gandiwa et al., 2014). The Afromontane vegetation dominates the park at high altitude and comprises fine-leaved dwarf shrubland (International, 2015). *Syzygium* is the dominant tree genus in the forests while *Brachystegia* woodland dominates in the drier and gentle areas where it is interspersed with grasslands. *Loudetia simplex* and *Themeda triandra* are the most common grass species in the reserve. On the granitic soils, *Vachellia* woodlands occur in isolated patches. Within this Afromontane forest-grassland mosaic the blue wildebeest (*Connochaetes taurinus*), waterbuck (*Kobus ellipsiprymnus*), kudu (*Tragelaphus strepsiceros*), plains zebra (*Equus quagga*), buffalo (*Syncerus caffer*), and southern reedbuck (*Redunca arundinum*) thrive

(Zisadza-Gandiwa et al., 2014). The greater part of Nyanga National Park consists of granitic soils interspersed with Umkondo Group dolerite and sandstone (Love, 2002). This study was carried out in Nyanga National Park within the former grassland section that is undergoing woody encroachment.

3.3.2 Intermediate rainfall sites

3.3.2.1 Lake Chivero Game Reserve

Lake Chivero Game Reserve was established in 1962 and occupies 1,867 ha (ZPWA, 2015). The Game Reserve is located 17°54′42″ South and 30°47′15″East. The mean annual rainfall at Lake Chivero Game Reserve is 829 mm. The rainfall regime is highly variable in time. The main vegetation type in the game reserve is Miombo woodland dominated by *Brachystegia spiciformis* and *Julbernardia globiflora* found in association with *Terminalia sericea, Parinari curatellifolia*, *Monotes glaber*, and *Burkea africana* (Malinga, 2001). The main herbivores found in Lake Chivero Game Reserve are eland (*Taurotragus oryx*), giraffe (*Giraffa cameleopardalis*), kudu (*T. strepsiceros*), blue wildebeest (*C. taurinus*), plains zebra (*E. quagga*), white rhinoceros (*Ceratotherium simum*), waterbuck (*K. ellipsipyrimnus*), southern reedbuck (*R. arundinum*), impala (*A. melampus*), and common warthog (*P. africana*).

3.3.2.2 Kyle Game Reserve

Kyle Game Reserve (KGR) was proclaimed a nature reserve in 1961 and covers an area of 4,400 ha. The game reserve is located at 20°11'20.01" South and 30°58'58.17" East. Altitude averages 1,050 m above mean sea level. The surrounding landscape consists of commercial farms to the north and communal land in the east. To the south and west, Lake Mutirikwi borders the game reserve. KGR receives a mean annual rainfall of 638 mm. Similar to Lake Chivero Game Reserve, the rainfall season is erratic. The dominant vegetation found in the north and south east of the reserve is Miombo woodland. *B. spiciformis* and *J. globiflora* dominate this woodland, whereas the bushland is dominated by *Dodonaea viscosa, Dichrostachys cinerea,* and the invasive *Lantana camara* (Masocha and Skidmore, 2011). Woodlands are open stands of trees that are at least 8 m tall with canopy cover of ≥40% without interlocking crowns while bushlands are characterised by woody species that are between 3 and 7 m tall and have a canopy cover of between 10 and 40% (Kindt et al., 2011) *Hyparrhenia filipendula* and *Hyperthelia dissoluta* are the predominant species in the open grassland areas (Vincent and Thomas, 1960). The main herbivores found in the reserve are common warthog (*P. africana*), buffalo (*S. caffer*), white rhinoceros (*Ceratotherium simum*), impala (*Aepyceros melampus*), giraffe (*G. cameleopardalis*), plains zebra (*E. quagga*), blue wildebeest (*C. taurinus*) and kudu (*T. strepsiceros*) (Masocha, 2010).

3.3.2.3 Ngezi Game Reserve

Ngezi Game Reserve is located at 18° 40' 59.12" South and 30°24' 0.68" East. The Game Reserve is 16,326 ha in area with 573 ha occupied by the lake. Mean elevation is 1,255 m. Ngezi was proclaimed a protected area in 1956. The average rainfall is 754 mm with most of it received between October and April. The greater part of the reserve is covered by *Brachystegia* Miombo woodlands interspersed with grassy vleis dominated by *Andropogon gayanus* and *Diplorhynchus condylocarpon.* The fauna of the reserve is made up of reintroduced indigenous mammals including several species of antelope such as southern reedbuck (*R. arundinum*). The serpentine soils with high levels of heavy minerals such as chrome and nickel dominate the reserve (Nyamapfene, 1991).

3.3.3 Low rainfall sites

3.3.3.1 Matopos National Park

Matopos National Park is located at 20° 30´ South and 28° 30´ East. It occupies a total area of 44,500 ha. The area was proclaimed a National Park in 1953 and has a mean annual rainfall of 618 mm. Matopos is closer to the dry end of the rainfall gradient than Kyle. Altitude ranges from 1,122 to 1,526 m. The dominant herbaceous species are *H. filipendula* and *H. dissoluta*. *Terminalia sericea* is the dominant tree species but is intermixed with *B. africana*. *Vachelia nilotica*, *V. karroo* and *V. rehmanniana* are also widespread in the park. The main herbivores found in the park are: black rhinoceros (*Diceros bicornis*), white rhinoceros (*C. simum*), klipspringer (*O. oreotragus*), steenbok (*Raphicerus campestris)* and common duiker (*Sylvicapra grimmia*) (Barry and Mundy, 1998). Sandy soils derived from granitic rocks dominate the Park with localised patches of organic soils and peat occuring on vleis and upland areas.

3.3.3.2 Tuli Safari Area

Tuli Safari Area (TSA) was established in 1958 as a controlled hunting area and was. proclaimed a protected area in 1975. TSA is located at 21° 58′ 13″ South and 29° 7′ 22″ East and forms part of the Limpopo-Shashe Transfrontier Park. Daily temperatures range from 5°C to 42 ° C while mean annual rainfall is 365 mm making it one of the driest protected areas in Zimbabwe. The vegetation is scrubland dominated by *Colophospermum mopane* and *Combretum molle* (Hyde et al., 2015). The genera *Enneapogon* and *Aristida* dominate herbaceous vegetation (Timberlake et al., 2002). The main herbivores found in TSA are kudu (*T. strepsiceros*), eland (*T. oryx*), impala (*A. melampus*), waterbuck (*K. ellipsiprymnus*), blue wildebeest (*C. taurinus*), zebra (*E. quagga*) and giraffe (*G. camelopardalis*).

3.4.1 Aerial Photographs

In this study we used 21 aerial photographs spanning a period of over 40 years to characterise woody encroachment across the six sites (Table 3-1). We used a single aerial photograph of the same site for each of the years considered up to the year 1996. The selection of a single aerial photograph per site was due to the non-availability of a complete set of aerial photographs across the sites for the study period. We thus, used all the available photographs for the study sites which had a complete time series. To cater for this limitation, we replicated the study at several sites spread along a rainfall gradient. All aerial photographs used in this study were acquired during the dry season to minimise the effects of radiometric differences due to changes in vegetation phenology and sun angle (Pittiglio et al., 2011). We considered the effect of different acquisition dates as negligible because the intensity-dominant scale approach used in this study is robust as demonstrated in the literature (Pittiglio et al., 2011). While fire could be a background factor that affects detection of woody cover in aerial photographs, we did not observe any fire and as such its influence on the results was considered insignificant.

Table 3-1: Date and scale of aerial photographs used for detection and characterization of woody encroachment across the six savanna landscapes in Zimbabwe. The scale presented in this table is resolution of the original imagery i.e., the ratio of a distance on an aerial photograph to that same distance on the ground in the real world

Site	Acquisition date	Scale (m)
Chivero	September 1972	1:25,000
	September 1984	1:25,000
	June1995	1:20,000
Kyle	August 1972	1:25,000
	June 1985	1:25,000
	August 1996	1:20,000
Matopos	June 1963	1:25,000
	June 1975	1:25,000
	August 1985	1:25,000
	August 1996	1:20,000
Ngezi	August 1965	1:25,000
	June1976	1:25,000
	September 1984	1:25,000
	August1996	1:20,000
Nyanga	June 1975	1:25,000
	September1987	1:25,000
	August1996	1:20,000
Tuli	June 1968	1:25,000
	June 1975	1:25,000
Tuli	June 1982	1:25,000
	August1996	1:20,000

Table 3-1 shows that the aerial photographs used had a similar scale i.e., the ratio of a distance on an aerial photograph to the corresponding distance on the ground in the real world.

We first scanned all aerial photographs using a ColorTrac Smart LF Ci40 scanner at a resolution of 1,200 dots per inch (dpi).Then, we imported the scanned aerial photographs in Integrated Land and Water Information System (ILWIS) (ITC, 2005), a remote sensing and GIS software. Next, we performed inner orientation. This involved referencing the four fiducial marks on the scanned aerial photograph based on the camera focal length, principal distance and scale information captured on the aerial photographs. This procedure establishes a geometric relationship between the coordinate systems of the aerial photograph and the instrument used for aerial photograph acquisition. After the registration of fiducial marks, we orthorectified the aerial photographs with the aid of scanned and geo-referenced 1:50,000 topographic maps as well as the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) 30 m digital elevation model. The aerial photographs were orthorectified based on the Universal Transverse Mercator Projection Zones 35 and 36 using Modified Clarke 1880 spheroid. Ground control points used for orthorectification were obtained from road intersections and fence corners visible on both the georeferenced topographic maps and the aerial photographs. Finally, we resampled the orthorectified aerial photographs for each site to the same georeference to north-orient the aerial photographs. The accuracy of the orthorectification was assessed using the root mean square error which was less than 0.5 m for all the aerial photographs.

3.4.2 Satellite Images

The formal acquisition of aerial photographs in Zimbabwe stopped in 1996. Therefore there were no aerial photographs covering the study area after this date. To fill this gap, we used six GEOEYE satellite images hosted on Bing Images (www.bing.com) spread across the study sites. All the satellite images for the study sites were acquired in 2011 except for Kyle which was acquired in 2012. The satellite images had a nominal spatial resolution of 1.64 m and were first converted to 8-bit greyscale using the colour separation algorithm in ILWIS GIS (ITC, 2005). The images were then resampled to the same spatial resolution (2 m) as aerial photographs to ensure comparability.

3.4.3 Wavelet transform

We determined changes in the linear dimension of dominant woody and grass patches using the Maximal Overlap Discrete Wavelet Transform (MODWT) based on the dominant scale (frequently occurring inter-patch distance where maximum contrast in dark and light tones is achieved) and intensity (the maximum contrast in dark and light tones) (Murwira and Skidmore, 2006). MODWT is a mathematical function that is implemented on images to detect the dominant scale at which features within an image such as woody cover occurs. Particularly, we performed wavelet transforms within the intensity- dominant scale framework based on tonal differences in aerial photographs and satellite images, to characterize woody encroachment in savanna ecosystems. In brief, a wavelet transform is an automated process that detects a match between the scale of observation and landscape features such as vegetation cover through the use of a moving window across the image. The moving window starts analysing the match between the scale of analysis and landscape features, at the smallest spatial scale up to the maximum possible scale equaling the size of the study area. In our case, we started analyzing this match between the scale of analysis and the window size from 2 m up to 256 m.

To determine the match between the scale of observation and the landscape feature such as woody or grass patches, we multiplied a wavelet function (moving window) with tonal variations in an image representing the spatial variation of vegetation cover in the landscape at increasing window sizes (Murwira and Skidmore, 2005). The wavelet is moved (translated) to various locations across the image containing the tonal variations and stretched (dilated) to quantify the local match of the wavelet to the signal (Addison 2002). Through this process we determined the location of the match between the moving window and the landscape feature including the scale at which this match was achieved (Pittiglio et al., 2011). In fact, the above steps result in an image of energy coefficients that quantify the match between the landscape feature and the window size at each spatial scale (Strand et al., 2006). Large positive or negative energy values are obtained when the moving window matches the shape of the signal representing features in the landscape. In contrast, a low positive product is obtained when the window size does not match the signal representing landscape features as captured on aerial photographs or satellite images under study. A detailed mathematical treatment of wavelets is covered in Ogden (1997).

Prior to performing wavelet transform, all the aerial photographs were resampled to a spatial resolution of 2 m to enable comparability of wavelet coefficients across the images over the years and to optimize computing space. The smallest scale of wavelet analysis corresponds to the grain of the aerial photograph which was 2 m in this study. We selected the maximum scale of 256 m based on our preliminary analysis which showed that there was no significant additional information that one gains from increasing the window size beyond 256 m.

3.4.4 Determining intensity and dominant scale

As mentioned earlier the wavelet transform yields an image with wavelet coefficients representing the match between the scale of analysis and the landscape features in an image. To make the coefficients comparable across spatial scales, we divided the sum of squares of wavelet coefficients at each scale by the total sum of the squares of wavelet coefficients at all spatial scales considered in this study. This yields normalised coefficients known as wavelet energy. We then determined the intensity and dominant scale by plotting the wavelet energy coefficients at each spatial scale on a scatter plot. The maximum energy value corresponds to intensity while the dominant scale is the spatial scale at which the maximum energy values occur (Murwira and Skidmore, 2005). All wavelet transforms were implemented in S-PLUS Version 8 (Insightful Corp).

3.4.5 Rainfall data

For each site, rainfall data were obtained from the Meteorological Services Department in Zimbabwe. At each site, we calculated the average rainfall for the previous 10 years prior to the acquisition date of either the aerial photograph or the satellite image. The rationale for this approach was that observations within remotely sensed data are a result of previous rainfall events. In this case 10 years was deemed sufficient for tree clusters to develop to such a size that they can be detected on an aerial photographs and satellite images. We then calculated the difference in mean annual rainfall between the successive time steps to determine decadal change in mean annual rainfall. The same approach was used to calculate changes in dominant scale and intensity.

3.4.6 Regression analysis

We used regression analysis to test whether changes in decadal mean annual rainfall significantly explain changes in dominant scale or intensity. Changes in dominant scale and intensity were treated as the response variables while changes in rainfall were treated as the predictor variable. Prior to regression analysis, we tested data for normality using Kolmogorov-Smirnov test. The results showed that changes in dominant scale did not significantly follow a normal distribution (P <0.05) while data for decadal changes in mean annual rainfall as well as changes in intensity followed a normal distribution (P > 0.05). We also tested whether the relationship between changes in mean annual rainfall and changes in dominant scale as well as between changes in mean annual rainfall and intensity were linear using a locally weighted scatter plot smoother (Cleveland and Devlin, 1988). The results showed that the relationship was non-linear. Based on these preliminary results, we then proceeded to use non-linear regression analysis to determine the relationship between changes in mean annual rainfall, dominant scale and intensity.

3.5 Results

3.5.1 Changes in intensity and dominant scale across the six savanna sites

From the 1960s to 2000s, we observed fluctuations in the intensity (maximum variance of woody cover) at all sites except one (Kyle) where an increasing trend was observed (Figure 3.3). For example, at the driest site in our study (Tuli), in 1968 the intensity was 0.25 %. This decreased to 0.21 % in 1975 but increased to 0.49 % in 1982 before decreasing again to 0.11 %. It then increases to 0.34 % in 2011. Increase in intensity suggests thickening of woody patches within the landscape that normally result from mass woody species recruitment and establishment associated with years of above normal rainfall (Holmgren et al., 2013, Kraaj and Ward, 2006, O'Connor et al., 2014a). The opposite is experienced during drought years when there is mass mortality of woody species that results in opening up of canopies leading to the expansion of grassland (Fensham and Fairfax 2007, Fensham and Holman, 1999, Twidwell et al., 2014, Bowker et al., 2012). Similarly, intense fires negatively affect growth and recruitment of woody species including seedling regeneration (Bond and van Wilgen, 1996, O'Connor et al., 2014a). In fact, studies have shown that tree cover is strongly reduced by fires (Starver et al., 2011). These processes create a relatively homogeneous grass layer with a few scattered trees and results in less contrast and hence low intensity in the landscape.

A similar pattern was observed for the dominant scale. We observed that the dominant scale, which is the scale at which maximum intensity of a patch is exhibited, fluctuated at three sites (Matopos, Kyle, and Ngezi). For example, at Matopos, the dominant scale detected in 1963 was 8 m. This increased to 128 m in 1975 reflecting expansion of dominant woody patches in the landscape. The dominant scale later decreased to 16 m in 1996. We also observed a stabilisation of dominant scale of 16 m at the wettest site (Nyanga) and at 4 m at the driest site (Tuli) (Figure 3.3).

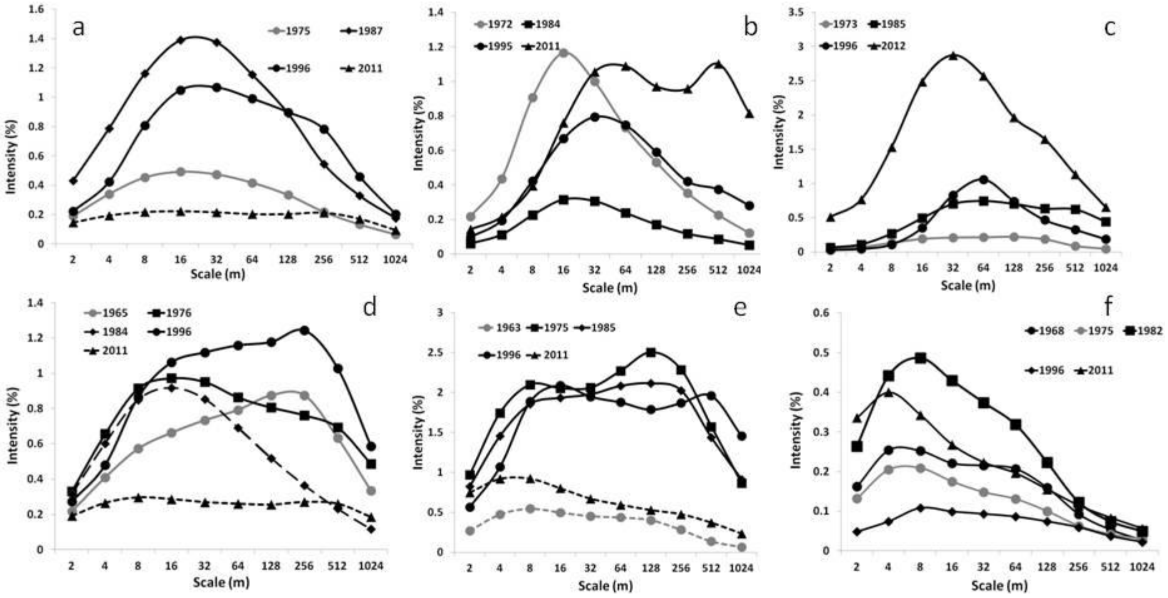

Figure 3.3: Changes in the dominant scale and intensity over time across the six savanna sites of Zimbabwe (a=Nyanga, b=Chivero, c=Kyle, d=Ngezi, e=Matopos and f=Tuli).

An increasing trend in dominant scale was observed at an intermediate rainfall site (Chivero) during the period 1972 to 2012 (Figure 3.3). For example, between 1972 and 1995 the increase in the dominant scale was driven by expansion of woody patches in the landscape. This expansion is visible on the aerial photographs (Figure 3.4).

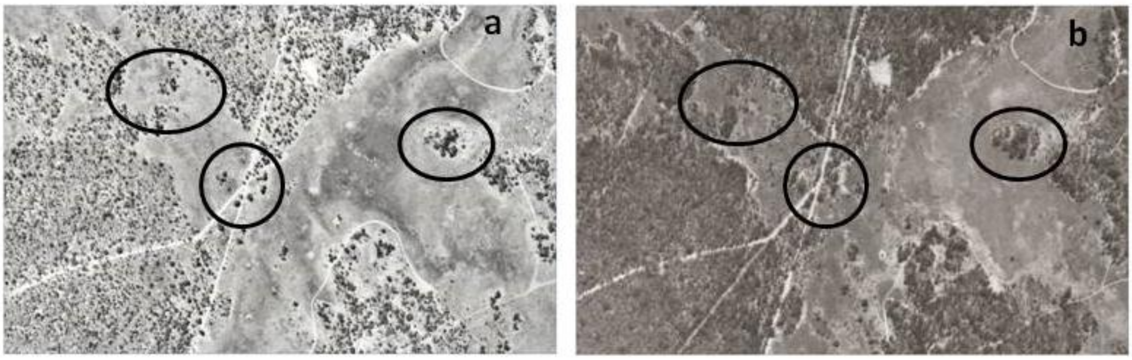

Figure 3.4: The increase in the extent and densification of woody patches at Lake Chivero game reserve between 1972 (a) and 1995 (b). Ovals locate areas where woody patches expanded and became denser. This increase in the spatial dimension of woody patches was detected via wavelet analysis as the increase in the dominant scale while densification of woody patches was captured through a change in intensity (refer to figure 3.3).

3.5.2 Relationship between changes in rainfall, dominant scale, and intensity

The relationships between decadal changes in mean annual rainfall, dominant scale and intensity of woody patches were inconsistent (Figure 3.5). A statistically significant non-linear relationship was observed between changes in decadal mean annual rainfall and dominant scale ($R^2 = 0.85$, $F_{13} = 35.9$, $P < 0.01$). Specifically, we observe that a negative change in dominant scale is associated with a decrease in rainfall while an increase or stabilisation in rainfall is associated with the stability or increase in dominant scale.

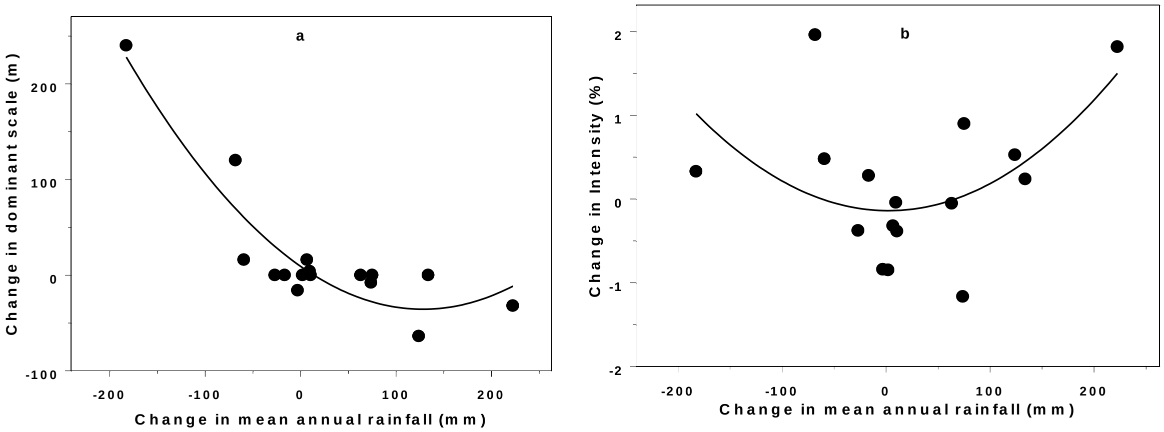

Figure 3.5: The relationship between a) change in mean annual rainfall and change in the dominant scale and b) change in rainfall and change in intensity, across six savanna sites of Zimbabwe.

A statistically insignificant non-linear U-shaped relationship was detected between changes in decadal mean annual rainfall and intensity ($R^2 = 0.29$, $F_{13} = 2.69$, $P = 0.106$). It can be observed that, changes in intensity, a measure of increasing contrast between woody patches and grass matrix, decreases with increasing decadal change in mean annual rainfall up to a point where intensity stabilises with stabilisation in mean annual rainfall. Beyond this stabilisation point, a net positive change in rainfall results in an increasing positive change in intensity.

3.6 Discussion

Results of this study indicate a significant but nonlinear relationship between decadal changes in rainfall and changes in the dominant scale. Specifically, larger negative changes in rainfall associate with bigger increases in dominant scale. Although the ecological mechanisms to explain this relationship are not yet clear, it is likely that decreases in decadal rainfall triggers mass tree and shrub mortality, which causes woody patches to shrink while grass patches expand due to reduced competition for resources, in particular, water. Thus, an increase in the dominant scale in a savanna landscape normally observed during drought years could be a reflection of the expansion of grass patches. Another interesting aspect of the results is that small changes in decadal rainfall are associated with a stable dominant scale in the landscape. On the other hand, larger increases in decadal rainfall are associated with a larger increase in the dominant scale in the landscape. Massive tree and shrub recruitment that is associated with pulses in rainfall availability lead to an expansion in the extent of woody patches which in turn causes the dominant scale to increase. Although this result may not be surprising (Sankaran et al., 2008, Buitenwerf et al., 2012), results of this study provide the first quantitative evidence on how decadal changes in mean annual rainfall relates with changes in the dominant scale of woody and grassy cover in a savanna landscape.

Results of this study indicate that changes in dominant scale are more sensitive to decreases in rainfall compared with increases in rainfall. This suggests that a decrease in decadal rainfall has heightened impacts on woody patches than an increase in decadal rainfall. This result has important implications for the management of woody encroachment in savannas as drought periods could be used as a window of opportunity for managing woody encroachment.

In our study, we could explain ~85 % of woody cover dynamics using only changes in decadal rainfall. This result amplifies the importance of rainfall as a key determinant of savanna tree-grass dynamics (Sankaran et al., 2005, 2008, Buitenwerf et al., 2012). Although rainfall could explain changes in the dominant scale at which woody patches occurred at the six sites, it could not significantly explain woody intensification. This result is contrary to expectation of a positive relationship between woody cover and density (Roques et al., 2001a). While we only assessed the effects of decadal changes in rainfall on woody cover and intensification in this study, we hypothesise that other factors such as fire could explain woody cover changes in the study area. Studies elsewhere have shown that fires in savannas tend to suppress woody cover through constraining tree recruitment and abundance (Higgins et al., 2007b, Aisling et al., 2015). Also, fire could affect woody intensification through top killing of woody seedlings and saplings (Sankaran et al., 2008). Thus, future studies need to assess the interactive effects of rainfall and other drivers such as fire in order to gain insights into tree-grass dynamics especially at smaller spatial and temporal scales.

Another important aspect of our results is that the dominant scale of woody patches seems to stabilise at the high and low ends of the rainfall gradient, i.e. humid and arid site respectively, while variability in dominant scale was experienced at sites with intermediate rainfall. The ecological explanation for this phenomenon is not yet clear thereby requiring further investigation. We thus propose that the stability in the dominant scale at both mesic and low rainfall sites could suggest the existence of buffering mechanisms that are stopping the tree-grass matrix from either transitioning to a grass or a wood dominated state (Jeltsch et al., 2000a). Since rainfall received at the mesic site (~1,200 mm per annum) is adequate for woody species recruitment, we deduce that the stabilisation of woody patch dimension at this site could be driven by factors other than changes in decadal rainfall. This would support the existence of an upper rainfall threshold beyond which other factors such as fire and herbivory regulate woody patch dynamics (Sankaran et al., 2005, 2008). At the dry site (~365 mm), woody species recruitment could be limited by rainfall as widely reported in the literature (Jeltsch et al., 2000, Sankaran et al., 2005). The six study sites we were all protected savanna sites thus limiting confounding effects of human and livestock disturbance on woody cover dynamics. Nevertheless, this does not rule out the potential role of other drivers such as fire or the role of wild herbivores (Groen et al., 2011).

Where our study differs from previous studies is in explaining changes in the dominant scale and intensity of woody cover as a function of changes in decadal rainfall. Even though changes in rainfall are known to be important in understanding woody encroachment (O'Connor et al., 2014), to the best of our knowledge no previous study has quantified the effect of changes in rainfall on changes in both the dominant woody patch dimension and changes in intensification. The approach used here allows one to explore the potential effects of climate change, in particular changes in precipitation patterns, on the rates of woody encroachment in tropical savannas. This could be a research priority given that the increases in rainfall variability are projected in southern Africa due to climate change.

Although our study observed that changes in rainfall explains ~85 % of the variation in dominant scale, an indicator of dominant patch size, we caution that other factors such as fire and herbivory could contribute to changes in both dominant patch dimension and intensity of woody patches in a savanna landscape. Previous studies Groen et al., (2011) have shown that small herbivores, though domesticated, negatively affect tree cover and variation in patch size. They further observed that high small herbivore densities could reduce the amount of tree cover as well as result in the disappearance of small patches. A recent study has emphasised the extermination of mega-herbivores as a driver of woody encroachment (O'Connor et al., 2014). We hypothesise that both small herbivores such as antelopes and mega herbivores could have a similar effect on woody cover as well as density in savanna ecosystems due to their browsing. In this regard, we recommend that future studies could consider other factors including changes in herbivore densities to test whether and to what extent they explain changes in the dominant scale of woody patches observed in savanna landscapes.

3.7 Conclusion

In this study we tested whether decadal changes in mean annual rainfall explain changes in dominant scale and intensity of woody patches at six protected savanna sites located along a rainfall gradient in Zimbabwe. We conclude that changes in the dominant scale of woody plant cover are significantly and non-linearly related to decadal scale changes in mean annual rainfall in Zimbabwean savannas. However, other drivers and processes occurring at smaller spatial scales could be regulating trends in woody encroachment reported in this study. In this regard, future work could test how projected changes in rainfall could influence woody encroachment at smaller spatial scale such as the neighbourhood scale where mechanisms governing plant to plant interaction can be experimentally assessed.

Chapter 4

Transitory effects of rainfall suppression and grass competition on the growth of *Vachellia karroo* sapling in a southern African savanna

This Chapter is based on:

Shekede, M.D., Murwira, A. Masocha, M and Gwitira, I., 2018. Transitory effects of rainfall suppression and grass competition on the growth of *Vachellia karroo* sapling in a southern African savanna. Paper submitted to the **African Journal of Ecology.**

Abstract

A decreasing trend in rainfall amount has been reported across southern African savannas but its effect on tree-grass interactions remains poorly understood. We used fixed-location rainout shelters to experimentally test the effect of a projected 15% decrease in rainfall on the growth of *Vachellia karroo* saplings in the presence of grass competition. Stem height and diameter were measured on the same individuals over a four year period at a semi-arid savanna site in Zimbabwe. Results indicate that during the first 15 months of the experiment, the mean diameter of saplings exposed to moisture stress was significantly ($p < 0.05$) higher diameter than that of the control plants. Similarly, grass competition significantly increased the basal stem diameter of *V. karoo* saplings but only up to about sixteen months (16) after the start of the experiment. Thereafter, no significant difference ($p > 0.05$) in stem diameter attributed to either rainfall suppression or grass competition was detected between the treatment and control groups. Over the entire experimental period, neither rainfall nor its interaction with grass competition affected sapling growth whether assessed using stem diameter or height. Combined, the results imply compensatory growth among *V. karroo* during the early stages of establishment in response to induced moisture stress and grass competition. The disappearance of significant growth effects after 15 months suggest that *V. karroo* saplings are able to alter allocation patterns in response to moisture stress and grass competition. However, long term field experimental studies are needed to provide more data to either confirm or refute whether this plasticity in growth buffers the plants against moisture stress in a changing climate.

4.1 Introduction

Savannas are moisture driven spatially and temporally heterogeneous ecosystems that comprise of a mix of grass species and woody species (Sankaran et al., 2008, Scholes and Archer, 1997a). Moisture availability controls woody species recruitment and growth (Aleman et al., 2016, Scholes and Archer, 1997a, van Langevelde, 2003), thereby determining tree-grass ratios in savannas. To this end, woody cover has been shown to positively respond to increasing rainfall (O'Connor, 1995, Sankaran et al., 2005a, Sankaran et al., 2008) with successful woody species establishment being recorded during periods of above normal rainfall (Kraaij and Ward, 2006a, O'Connor et al., 2014b). In contrast, there is evidence of mass mortality of woody vegetation during drought periods further indicating the sensitivity of savannas to changes in moisture availability (Adams et al., 2009, Fensham et al., 2009, Twidwell et al., 2016b). Thus, an understanding of how savanna ecosystems respond to specific changes in moisture availability is critical for their management.

Global Circulation models (GCMs) project that rainfall could decrease by different magnitudes, i.e., ~4-30% in southern African savannas, as a result of climate change (IPCC, 2014a, IPCC, 2007). Furthermore, temperatures are projected to rise thereby resulting in increased aridity in southern African savannas (IPCC, 2007, IPCC, 2014a, Shongwe et al., 2009). Thus, the projected decreases in rainfall, combined with increases in temperature, may have significant impacts on the savanna ecosystems, yet it is currently not clear how and whether the anticipated decrease in rainfall will alter tree-grass interactions in savanna ecosystem.

Semi-arid savannas that are predominant in Southern Africa are located closer to the lower end of the rainfall gradient (Chamaillé-Jammes and Fritz, 2009, Sankaran et al., 2008). Therefore, it is reasonable to hypothesise that any rainfall decreases may significantly alter tree-grass coexistence in semi-arid savannas (Huxman et al., 2004). This is in contrast to mesic savannas where a decrease in rainfall may not necessarily be expected to lead to significant structural changes since water may not be limiting. (Sankaran et al., 2008). Given these possible but conflicting outcomes, it is critical to gain a mechanistic understanding of the potential effects of the projected moisture decline on the structure of savannas.

In this study, we experimentally tested the effect of a reduction in rainfall and grass competition on the growth of Vachellia karroo (*V. karroo* formerly *Acacia karroo*) saplings over a four year period at a semi-arid savanna site in Zimbabwe. The selection of *V. karroo* as our focal species in the experiment was motivated by the fact that it is one of the key species in southern African semi arid to arid savannas (O'Connor et al., 2014b).

4.2 Materials and Methods

4.2.1 Study area

A field experiment was set up at a protected semi-arid savanna site at Kyle Game Reserve (KGR) in Zimbabwe to test the effect of rainfall decline on the growth of *Vachellia karroo* (Hayne, Banfi & Galasso) saplings. The experiment station was fenced off using a combination of barbed wire and diamond mesh wire to exclude large and small mammal herbivory (see Plate 4.1).

Plate 4-1: A side view of a fenced experimental station established at Kyle Game Reserve in Zimbabwe to test combined effects of rainfall and grass competition on the growth of *Vachellia karroo* saplings.

The game reserve is located at 20◦06′ of latitude South and 30◦58′ of longitude East (Shekede et al., 2015). The average altitude is 1,050 meters above sea level. Rainfall is characterised erratic and relatively low with a mean annual value of 638 mm (Figure 4.1). Over the four year duration of the experiment, two years i.e., 2012 and 2015 received below normal rainfall. Mann Kendal test results indicate a negative trend in rainfall for this site although this is not significant (tau=-0.241181, p=0.15). Figure 4.1 illustrates a positive trend in both minimum temperature (tau=0.006, p=0.972) and maximum temperature (tau=0.497, P=0.003) at the study site.

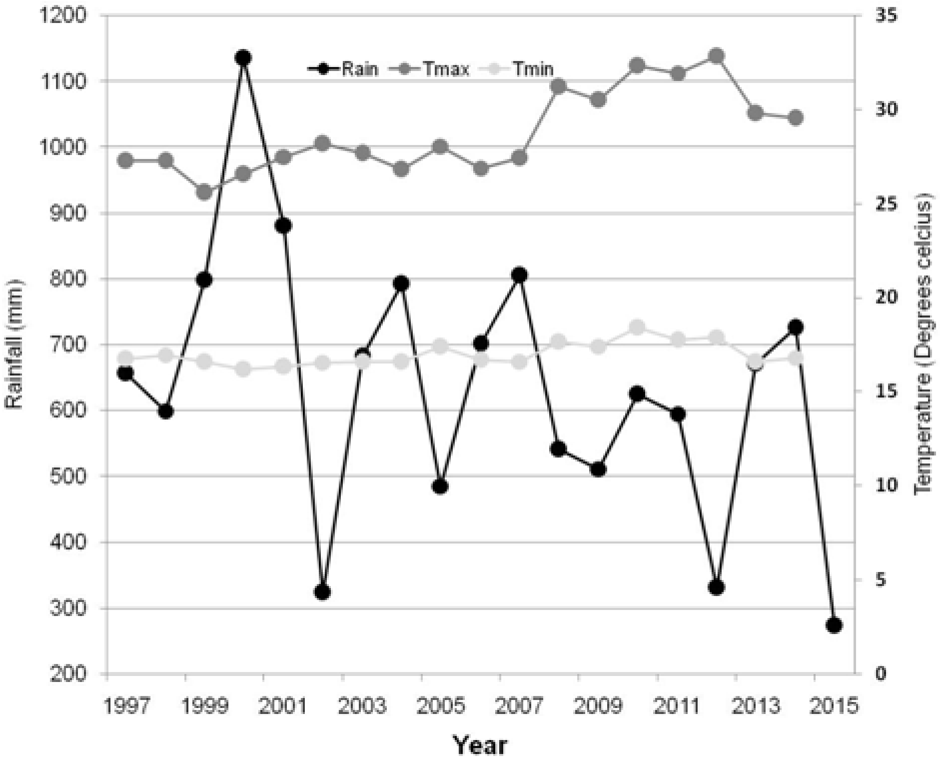

Figure 4.1: The minimum temperature (°C), maximum temperature (°C) and rainfall (mm) for Kyle Game Reserve between 1997 and 2015. (Source: NASA POWER Project https://power.larc.nasa.gov/cgi-bin/agro.cgi?email=agroclim@larc.nasa.gov. Data accessed on 31 October 2016).

The dominant soils are clays derived from basalts (Masocha et al., 2011). Woody vegetation is dominated by *V. karroo* and the invasive *Lantana camara L*. (Masocha and Skidmore, 2011) while *Hyparrhenia filipendula* (Krauss) Stapf and *Hyperthelia dissoluta* (Nees) Clayton (Vincent and Thomas, 1960) are predominant in the open grassland areas. The common game species at the study site include common warthog (*Phacochoerus africanus*), African buffalo (*Syncerus caffer*), southern white rhinoceros (*Ceratotherium simum simum*), common impala

(*Aepyceros melampus*), giraffe (*Giraffa cameleopardalis*), plain zebra (*Equus burchelil*), common eland (*Taurotragus oryx*) and the greater kudu (*Tragelaphus strepsiceros*).

4.3 Future projections of rainfall for southern Africa

Although predictions of rainfall in future climate differ widely among Global Climate Models (GCMs) in terms of the magnitude and direction of change in rainfall in southern Africa, a number of these GCMs show that southern Africa is likely to experience a reduction in rainfall towards the end of the 21st century (IPCC, 2007). Table 4.1 provides an overview of the projected changes in rainfall in southern Africa. Given these varied projections for the region, we designed our fixed rainout shelter to intercept around 15% of the incident rainfall, which is the median percentage decrease in rainfall and lies within the range of the predicted rainfall for the southern Africa in the coming decades.

Table 4-1: Projected changes in rainfall in southern Africa

Source	Projected average decrease (%)
IPCC 2001	15
IPCC 2007	12
Jury (2013)	15
Mitchel and Tanner(2006)	15
Kurukulasuriya and Mendelson (2006)	15.5
(WorldBank, 2013)	30
Average projected rainfall decrease	15

4.4 Experimental design

Forty eight *V. karroo* saplings of the same size class (Mean diameter= 0.73±0.2 cm, Mean height=58.35±13cm Standard Deviation) and same age cohort were selected at Kyle Game Reserve in October 2012. The experiment consisted of two main treatments each with two levels, that is, 1) rainfall suppression versus natural rain, and 2) grass competition versus no grass competition, which were crossed. Based on IPCC (2007) projections for southern Africa, two rainfall treatments i.e., the control (no rainfall suppression) and a 15% rainfall suppression treatment were applied to *V. karroo* saplings. Each treatment was replicated six times to yield a total of 12 experimental units. These rainfall treatments were designed to address the expected decreases in rainfall over southern Africa. For the grass competition, two main treatments were applied. These were grass competition in which grass (both annuals and perennials) was left intact in the experimental plots and the control in which all herbaceous vegetation was removed through clipping at ~2cm above the ground. Each grass treatment was replicated 6 times to yield 12 experimental units. The remaining saplings were exposed to other treatments (fertilisation) which are not reported in this paper. The selection of *V. karroo* species was based on the observation that it is one of the key encroacher species in savannas (O’connor et al, 2014) and constitutes a significant proportion of vegetation cover in the Game Reserve.

Fixed-location rainout shelters (Yahdjian and Sala, 2002) covering an area of 3.76 m2 were constructed using bands of transparent acrylic mounted on a metal frame to mimic a 15% decrease in rainfall at each experimental site as illustrated in Figure 4.2. The metal frame was 2 m long and 1.88 m wide. The height of the rainout shelter was 45 cm at the back and 113 cm on at front thus forming a 20° roof inclination (Yahdjian and Sala, 2002). The 15% reduction was achieved through blocking 15% of the area of the rainout shelter using strips of acrylic material. Specifically, three corrugated acrylic strips with a width of 10 cm and 188 cm long were interspersed at a distance of about 66.5 m from each other to achieve 15% coverage of the plot. The fixed-rainout shelters were designed in such a way that the target saplings were at the centre of the structure.

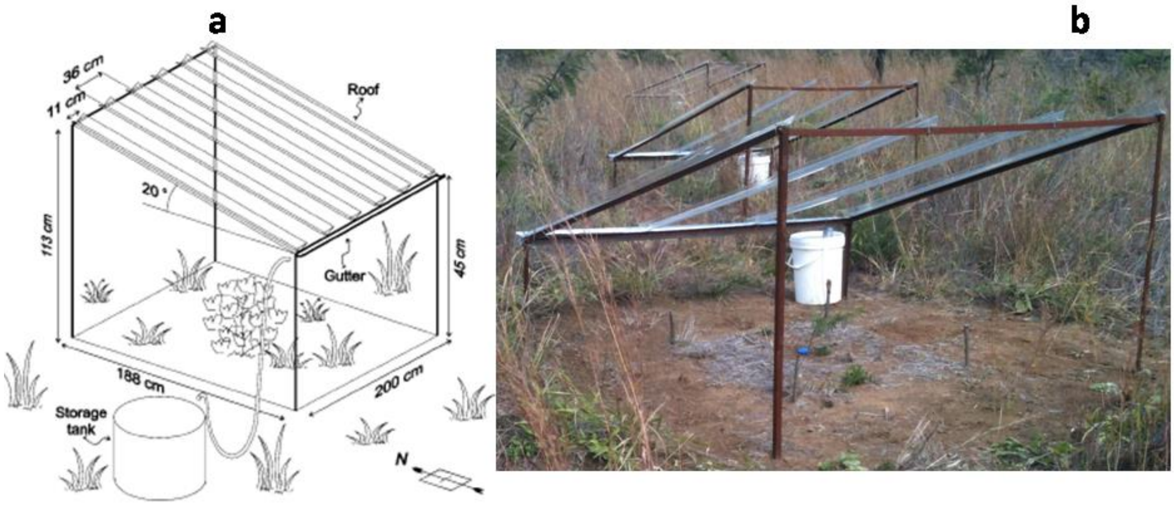

Figure 4.2: The design and a photograph of a standard rainout shelter used to reduce rainfall by 15% during the field experiment at Kyle Game Reserve in Zimbabwe.

Previous work reported that rain-out shelters have a tendency to change the microclimate such as temperature or solar radiation (Jacoby et al., 1988). To eliminate these effects, the sides of the rainout shelter were left open to allow for free air circulation and minimize temperature and humidity artefacts (Fiala et al., 2009). In addition, acrylic bands used in this study allowed light penetration and thus they did not cause any form of shading over the experimental plants. Note, a previous study that has assessed differences in microhabitat conditions in and outside the rainout shelters of the same design concluded that temperature, humidity and soil moisture were not significantly affected by the design (Fiala et al., 2009). Considering that the rainout shelters covered a relatively small area (3.76 m2), to ensure that subsoil lateral water flow did not affect the experiment, water from the rainout shelters was diverted using gutters. The gutters directed water into 30-litre white plastic containers that were emptied after each rainfall event. In addition, to minimise potential extraction of moisture from areas outside the fixed-rainout shelters, the rainout shelters were designed in such a way that the target saplings were at the centre of the structure. Because target saplings were located at the centre of the plot, it was assumed that the buffer area of 2.76 m2 was sufficient to minimise foraging of resources outside of the rainout shelter. The control plots had no rainout shelters and thus received normal rainfall.

4.5 Data collection

Two growth metrics, that is stem height change and diameter increases were used to assess effects of the treatments on sapling growth. At the end of every month, stem diameter was measured on each individual at the base using a vernier calliper while stem height was measured from the ground to the tip of the stem using tape measure and a, respectively. For consistency and to allow repeated measurements on the same individual, each stem was assigned a unique numerical label inscribed on a small metal disk, which was placed inside the plot.

4.6 Data Analysis

At the start of the experiment data for sapling height and basal diameter were obtained and tested for significant differences using the student-t test. Both sapling stem diameter (t_{10}=-0.153574, p>0.05) and height (t_{10} = -0.13, p>0.05) selected for the rainfall treatment and control showed no significant differences at 95% Confidence level. Similarly there were no significant differences (p>0.05) in the height and diameter of plants grown in the presence and absence of grass competition at the start of the experiment. Following the test of data for normality using Kolmogorov-Smirnov test and having found that data did not significantly deviate from a normal distribution, repeated measures analysis of variance (ANOVA) was then used to test whether changes in basal diameter and stem height of *V. karroo* differed significantly among the rainfall and grass treatments over time. The data were analysed in STATISTICA Version 8 statistical software (StataCorp, 2003).

4.7 Results

4.7.1 Effects of time and rainfall suppression on the diameter of *V. karroo* saplings

Figure 4.3 illustrates the effects of a 15% reduction in rainfall on the diameter of V. karroo over time. The response of saplings to rainfall manipulation varied over time although there was a general increase in the sapling diameter. In particular, the diameter of treatment saplings increased faster than the control with some crossovers observed at about fifteen months to twenty months after the start of the experiment. There was a significant effect of time on diameter (F_{10}=3.72, P=0.00). The interaction effect of time and rainfall was also significant (F_{10}=3.72, P=0.01) but the main effect of rainfall on sapling diameter was not significant (F_1=1.72, P=0.24) during the first 15 months of the experiment. Figure 3 further illustrates that after 15 months, the diameter of the treatment saplings in the treatment group expanded faster than that of plants in the control group up to 40 months. Beyond 40 months, the growth trajectory between the treatment and control groups was similar. Even after 15 months, the main effects of rainfall on sapling diameter remained insignificant (F_1=0.04, P=0.86). In contrast, the interaction effects of rainfall and time which were significant during the first 15 months of the experiment became insignificant (F_{29}=1.06, P=0.40).

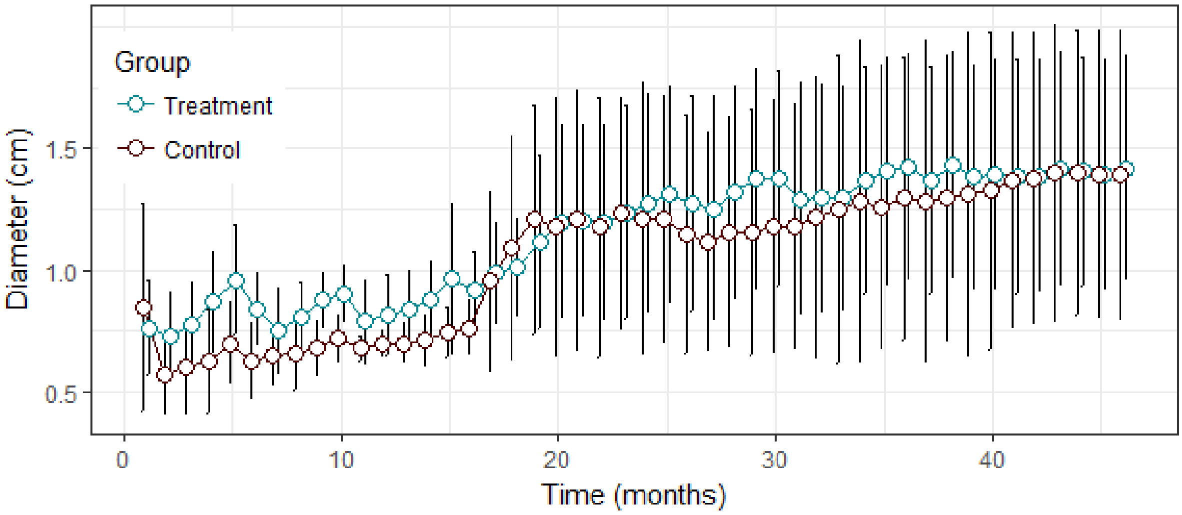

Figure 4.3: Effect of rainfall suppression on stem diameter of V. karroo saplings at Kyle Game Reserve over a four year period. Errors bars indicate mean ± Standard Deviation. The Control group comprised saplings growing under natural rainfall conditions while the treatment group comprised saplings exposed to a 15% reduction of rainfall.

The results of repeated measures ANOVA assessing the main and interaction effects on rainfall suppression and time on the growth of *V. karroo* saplings are shown in Table 4-2. The results reveal non-significant main effects of rainfall on stem diameter changes. The interaction effects of rainfall and time were also not significant but the effect of time was significant.

Table 4-2: Repeated measures ANOVA table showing effects of time as well as a 15% rainfall decrease on the diameter of V. karroo saplings over a four year period.

Source	SS	DF	MS	F	P
Intercept	1,540,565	1	1,540,565	75.88	0.000
Rainfall	6,117	1	6,117	0.30	0.603
Error	121,807	6	20,301		
Time	80,464	45	1,788	9.79	0.000
Time * Rain	5,909	45	131	0.71	0.909
Error	49,274	270	182		

4.7.2 Effect of grass competition on diameter of V karroo saplings

Figure 4.4 illustrates variation in the mean diameter (± SD) of *V. karroo* saplings grown in the presence of grass competition. The data in figure 4 indicates that grass competition did not significantly affect the basal diameter of *V. karroo* saplings over the duration of the experiment (F_1=0.10, P=0.755). Although not statistically significant, during the first 16 months, the mean diameter of saplings growing under grass competition was larger than that of control plants that grew in the absence of grass competition.

Results of repeated measures ANOVA confirmed that the interaction of grass competition and rainfall was not significant (F_1=0.14, P=0.711) just as the interaction of grass competition and time was (F_{45}=0.49, P=0.998). Further, results of repeated measures ANOVA indicated that the three way interaction of time, rainfall and grass competition did not significantly affect stem diameter (F_{45}=0.89, P=0.676) over the duration of the experiment. However, time alone (F_{45}=8.711, P=0.00) as well as the interaction of time and grass competition (F_{15}=1757, P=0.042) significantly explained variation in the basal diameter of *V. karroo* up to about sixteen months (16) from the start of the experiment (Figure 4.4). Beyond 16 months, the mean diameter of saplings growing in the absence of grass competition (control group) was consistently higher than that of saplings exposed to grass competition.

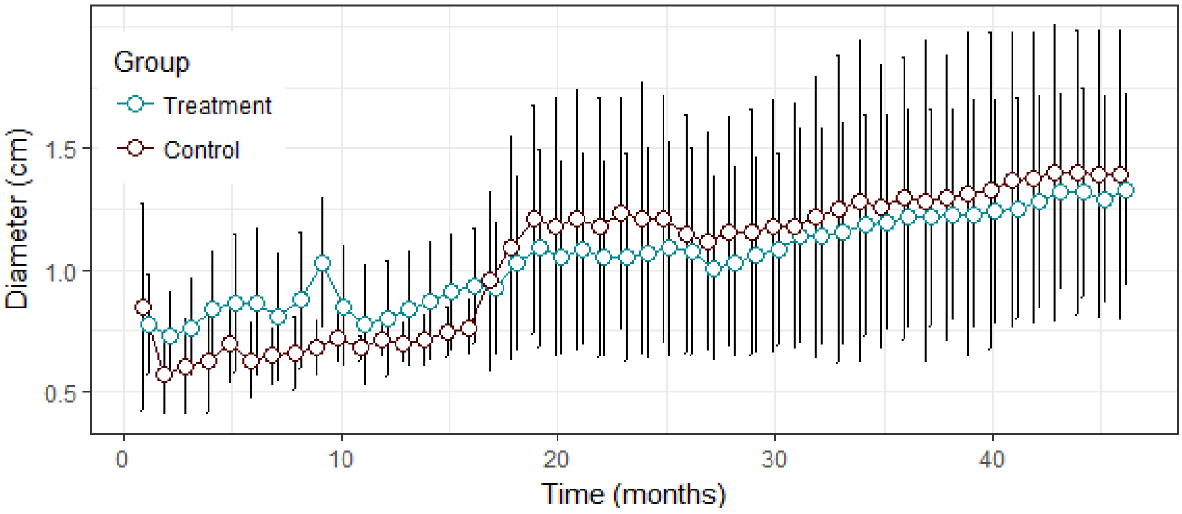

Figure 4.4: Effect of grass competition on stem diameter of V. karroo saplings at Kyle Game Reserve over a four year period. Errors bars indicate mean ± Standard Deviation. The Control group comprised saplings growing without grass competition while the treatment group comprised saplings exposed to grass competition.

4.7.3 Effect of rainfall suppression on height growth of V. karroo saplings

Figure 4.5 shows that the response of *V. karroo* saplings to rainfall suppression varied over time with both the treatment and control groups decreasing during the first five months following the installation of the experiment in October 2012. The stem height then stabilised for about eight months before increasing. Thereafter, stems in the treatment group was consistently shorter compared to those in the control group with the differences becoming larger after 35 months.

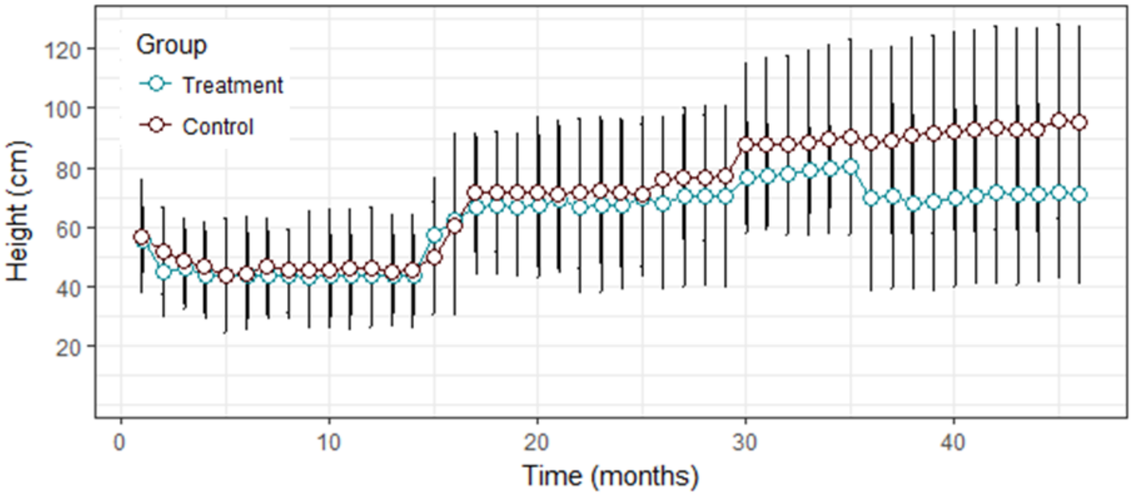

Figure 4.5: Effect of rainfall suppression on stem height of *V. karroo* saplings at Kyle Game Reserve over a four year period. Errors bars indicate mean ± Standard Deviation. The Control group comprised saplings growing under natural rainfall conditions while the treatment group comprised saplings exposed to a 15% reduction of rainfall.

Table 4-3 shows the result of repeated measures ANOVA performed to test main and interaction effects of rainfall suppression and time on stem height of *V. karroo* saplings. Similar to the effects observed on sapling diameter, rainfall suppression (F_1=0.17, P>0.05) and its interaction with time (F_1=0.23, P>0.05) did not have significant effects on *V. karroo* stem height (Table 4-3). In contrast, time had significant effects on stem height (F_{44}=8.13, P=0.00). The intercept in the repeated measures ANOVA model was also significant (F_1=87.6, P=0.00).

Table 4-3: Repeated measures ANOVA table showing effects of time as well as a 15% rainfall decrease on stem height of V. karroo saplings over a four year period.

Source	SS	DF	MS	F	P
Intercept	411.81	1	411.81	87.60	0.00
Rainfall	0.78	1	0.78	0.171	0.69
Error	28.20	6	4.70		
Time	22.19	44	0.50	8.13	0.00
Time*Rainfall	0.64	44	0.01	0.23	1.00
Error	16.37	264	0.06		

4.7.4 Effect of grass competition on the height increment of *V. karroo* saplings

Figure 4.6 illustrates the growth of woody saplings under grass competition over the duration of the experiment. In the first three months of the experiment, saplings in the control group were taller than saplings in surrounded by grasses. Although the differences were not significant, between the 4th and 30th months, faster stem height increment was consistently observed in the treatment group. The differences in mean stem height between the treatment and control groups became smaller 30 months suggesting similar growth patterns.

Overall, saplings growing under grass competition had shorter stems (mean = 71±11.1cm SE) than those in the control group where grass competition was excluded (mean stem = 75.5±5.6cm SE). However, neither grass competition alone (F_1=1.266, P=0.279) nor its interaction with rainfall suppression (F_1=0.033, P=0.858) significantly influenced the height increment of *V. karroo* saplings.

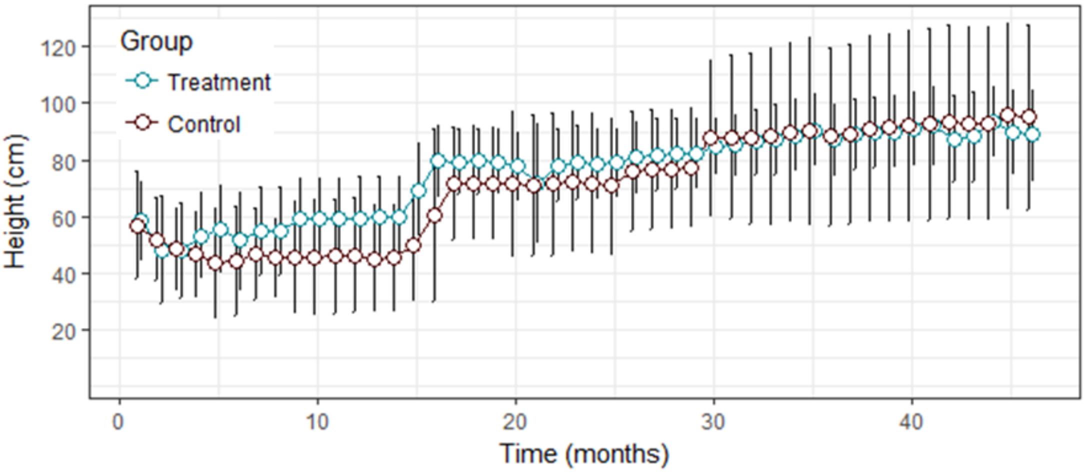

Figure 4.6: Effect of grass competition on stem height of V. karroo saplings at Kyle Game Reserve over a four year period. Errors bars indicate mean ± Standard Deviation. The Control group comprised saplings growing without grass competition while the treatment group comprised saplings exposed to grass competition.

4.8 Discussion

Results of this study underscore the importance of temporal analysis of the effects of rainfall induced stress on sapling growth to understand potential effects of climate change on tree-grass interactions in savanna ecosystems. While the overall effects of rainfall suppression on *V. karroo* sapling growth were found to be insignificant over a 46 month experimental period in which rainfall was reduced by 15% under field conditions, the present study isolated periods in the growth of *V. karoo* saplings in which suppressing rainfall interacted with time to cause a significant effect on sapling growth. These important ecological effects during the critical establishment phase of saplings could have been easily missed if a short-term experiment was undertaken.

Mixed results were obtained depending on whether the focal metric of growth was basal stem diameter or stem height. For instance, during the first 15 months of experiment the mean diameter of saplings growing under natural rainfall conditions (control group) was consistently smaller (0.685±0.16cm (SD) than that of the treatment group growing under suppressed rainfall conditions(0.845±0.18cm (SD). By contrast, the mean stem height of treatment plants measured at the base was observed to be larger (83.277±9.3 cm (SD) than that of the control group (71.113±4.11cm (SD) from the 17th month to the end of the field experiment. These results suggest that plants growing under suppressed rainfall allocated more energy towards diameter growth as opposed to height increment resulting in increased allocation to roots. The results imply that in response to moisture stress, *V. karroo* saplings tend to prioritise root foraging (Archibald and Bond, 2003, Poorter and Nagel, 2000). This is in partial agreement with previous work that reported a reduction in the diameter and height of woody species under an experimental imposed drought in a southern savanna (Van Der Waal et al., 2009).

It is also important to note that while Van Derv Waal (2009) reported that drought reduced both root biomass and stem height, in the present study, though not statistically significant, moisture stress favoured diameter expansion. This corroborates the work of Padilla et al., (2009) which found that water manipulation tend to significantly affect roots but not growth of shrubs in a green house experiment. In a similar study, Chirara (2001) demonstrated that the *V.karroo* seedlings intensively invested in root growth and reached a minimum length >56cm within the first two months after emergence, a strategy that is critical for the survival of the species in the presence of drought and grass competition. However, the inference that under moisture stress saplings tend to allocate more energy to roots needs to be treated with caution since belowground measurements were not recorded as this would have entailed destructive sampling. Nevertheless the mechanism proposed to explain stem diameter increase under moisture stress may hold since it is difficult to envisage an allometric pattern in which root biomass can increase without a corresponding increase in the base of the stem.

The disappearance of the effect of rainfall suppression observed after fifteen months is an unexpected result which may be attributed to the fact that the 15% reduction in rainfall could be insufficient to cause discernible impacts on the growth of the target species as it falls within the normal rainfall variation of the area (Coefficient of variation =33%). Previous studies have demonstrated that plants subjected to moderate moisture stress can grow at the same rate as plants growing under normal rainfall conditions though with a slight increase in Root Mass Fraction i.e., the ratio of root dry mass divided by total plant dry mass (Padilla et al., 2009, Poorter et al., 2012). In fact, investment in deep roots soon after establishment confers resilience to *V.karroo* thereby enabling the woody species to withstand fluctuations in moisture availability in semi-arid tropical regions that are characterised by erratic rainfall (Chirara, 2001). It is only when plants are subjected to severe moisture stress that there may be an increase in allocation to roots at the expense of stems (Poorter et al., 2012). In this study, there were instances in which stem diameter and height decreased as a result of drought induced moisture stress. For instance, drought that was experienced in 2012 led to dieback in some sapling resulting in reduction in height especially in the first three months after the start of the experiment.

Drought-induced dieback has been widely reported in ecosystems across the globe (Allen et al., 2010, Anderegg et al., 2015, Byer and Jin, 2017, Klein, 2015, Tafangenyasha, 1998). In this regard, future work could focus on carrying out experiments in which multiple levels of water regimes are manipulated in order to determine the threshold beyond which water reduction will significantly affect woody species growth. Moreover, future rainfall manipulations need to be sensitive to rainfall variability since rainfall in southern Africa is highly variable in space and time. This information could be critical for understanding the levels of precipitation decreases that are likely to change tree-grass mosaics characteristic of the savannas.

Results indicated significant effects of time and its interaction with rainfall on the diameter of *V. karroo* saplings during the first 15 months after the start of the experiment with no significant effects thereafter. This result suggests that the early stages of woody species recruitment might be more sensitive to changes in moisture availability than the later stages of growth (Bond, 2008). In fact, wet season droughts are the major drivers of germinant mortality regardless of presence or absence of grass competition (Bond, 2008). Early stages of woody recruitment are therefore the most critical as they determine whether the species will increase in abundance and thereby determine ecosystem structure and function (Woods et al., 2014). Moreover, the majority in both stem diameter and height growth occurred in a distinct pulses coinciding with rainfall season (e.g., months 15-19; December 2013 to April 2014) thereby confirming that savannas are water limited ecosystems (Sankaran et al., 2008). However, since the experimental design was such that the treatment plants were exposed to 15% less rainfall than the control, the results for this study may be difficult to extrapolate for values greater than 15%.

In this study it was found out that, overall, the growth of *V. karroo* saplings i.e., both the diameter and height were not significantly affected by the presence of grasses. These results are inconsistent with several studies that observed negative effects of grass competition on the growth and establishment of woody saplings in savannas (Riginos, 2009, Vadigi and Ward, 2013, Cramer et al., 2010, Mopipi et al., 2009b, Melina et al., 2015). Based on Walter's two layer hypothesis, studies have shown that woody saplings compete with grasses for resources such as water, light and nutrients with grasses being better competitors at seedling stage since grasses are efficient in exploiting nutrients and water in the top soil layer relative to saplings (Sankaran et al., 2005, Sankaran et al., 2008, Scholes and Archer, 1997a). However, the reduction in suppressive effect experienced after the first three months may indicate the transitory competitive tree-grass interactions in response to changes in resource availability typical of savannas. Since grasses growing at the experimental site were already established it was expected that grasses would exert greater suppressive effects on woody sapling growth. However, it is not unusual to detect no effects of grasses on the growth of woody saplings (van Auken et al., 1985).

Another unexpected result in this study is that after the first three months saplings grown in competition with grass were taller than saplings in a monoculture. In this study, the suppressive effects of grasses on the height increment disappeared after the first three months before reappearing at 30 months. In contrast, the suppressive effects of grasses on the diameter of woody saplings only appear after 17 months after the start of the experiment. Although not explicitly tested in the experiments, taken together these results suggest adjustment of energy allocation patterns by woody species in response to grass competition for limiting resources. Furthermore, results from this study could be providing evidence of dynamic nature of positive and negative interactions in savanna ecosystems (Maestre et al., 2003).

Results from this experimental study showed that woody saplings were not significantly affected by grasses regardless of whether rainfall was reduced or not. This observation contradicts findings by Riginos (2009a) who showed that grass competition significantly reduced growth and recruitment of trees irrespective of the demographic stage or rainfall amount. In this study, although not significant, the shift in suppressive effect of grasses on woody sapling growth over time might suggest the transitory nature of interactions between grasses and woody species in savannas. For the greater duration of the experiment grasses seem to have had a positive effect on woody seedling. While the mechanism driving this phenomenon is not clear, it could be that the interaction between grasses and trees could have shifted from competitive to facilitative and vice versa under fluctuating rainfall amounts. The results from this study are in accord with the Stress Gradient Hypothesis that predicts increasing role of positive interactions under conditions of high environmental stress (Bertness & Callaway 1994). Moreover, in agreement with previous studies, results of this study could be suggesting that grass swards ameliorate soil and ambient temperatures through providing shade thereby facilitating the growth of woody saplings (Joubert, 2014). For, instance, shading enhances *Vachellia karroo* sapling growth through ensuring gradual recession of the moisture zone to deeper layer where the woody species can access moisture for longer periods due to its long tape root (Chirara, 2001). Overall, saplings escape herbaceous competition mainly through niche differentiation via root growth, biomass allocation as well as morphological changes.

This experimental study considered two factors that affect woody species recruitment in savannas namely rainfall and grass competition. However, other factors such as fire and herbivory are also important in limiting woody species recruitment. Studies have shown that successful recruitment of savanna saplings is constrained through ‘topkill’ by herbivores and fire (Bond, 2008, Bond et al., 2003a, Higgins et al., 2007a). Through this mechanism saplings are often prevented from transitioning into large size class resulting in dominance of short and juvenile plants (Higgins et al., 2007a). To escape fires, saplings can either quickly grow to a height that is above the flame zone in time before the next fire or allocate resources to thick heat-insulating barks that are fire resistant (Dantas and Pausas, 2013). Herbivory has similar effects to fires in that it reduces the growth as well as transitioning of saplings into adult plants (Dantas and Pausas, 2013). Fire suppression (Lawes et al., 2011) and the extermination of mega-herbivores (O'Connor et al., 2014) have cited as key drivers of woody encroachment across the globe. In this study large herbivores and fire were excluded at the study site through the fencing and fire guards, respectively.

Where our study differs from previous research is on the manipulation of natural rainfall under field conditions in a southern African savanna ecosystem using rainout shelters over a relatively longer time scales than most studies that have used similar approach (see Barbosa et al., 2014a, Throop et al., 2012). In fact, most experimental studies on testing the potential effect of rainfall decreases as a result of climate change on savanna ecosystems were short-term i.e., less than two years (Barbosa et al., 2014, Otieno et al., 2010) and few studies focused on African savannas (Barbosa et al., 2014, Beier et al., 2012, February et al., 2013, Kulmatiski and Beard, 2013, Otieno et al., 2010, Wu et al., 2011). In fact, our study is among the few that have manipulated rainfall using rainout shelters that mimic the projected decrease in rainfall in southern Africa. For instance, previous rainfall manipulation studies imposed reductions of up to 150% on locally abundant tree seedlings in a southern African savanna site, yet these rainfall manipulations could be well beyond what is projected by most climate models (February et al., 2013). In this regard, the failure to mimic the projected changes in rainfall may overstate the potential impact of climate change on savanna ecosystem. An additional strength of the current work relates to repeated measurements made on the same individuals, though few, over a relatively long period (4 years). This approach permitted teasing out significant but transient effects of rainfall suppression among saplings at the crucial establishment stage.

A limitation of this study is that standard rainout shelters measuring 2 m in length and 1.88m in width were used to reduce by approximately 15% the amount of rainfall experimental plants received. While the rainout shelters were effective in redirecting rainfall away from the target *V. karoo* saplings, it cannot be ruled that saplings might have extracted moisture outside of rainout shelters due to their extensive roots (Barnes et al., 1996, Wigley et al., 2009, Archibald and Bond, 2003) or benefited from lateral flow. Since, root length and spread and lateral flow were not directly measured in this experiment, our results might have the confounding effect of root foraging outside the rainout enclosures as well as lateral flow and this underscores the need to improve the design of rainout shelters in future work to guarantee ‘clean’ results. Thus, while caution is needed in interpreting the results of this study given the above limitation, it has to be pointed out that all *V. karroo* plants used in the experiment were saplings. Therefore, it is likely that their root system might not have fully developed to the extent that the effects of reducing the amount of rainfall might have been cancelled out by considerable foraging for moisture outside rainout shelters or in the deeper soil layers. Moreover, previous studies demonstrated negligible effects of a similar rainout shelter on soil moisture and humidity (Fiala et al., 2009, Yahdjian and Sala, 2002).

4.9 Conclusion

This study tested the extent to which a 15% rainfall suppression affect the growth of *Vachellia karroo* in a semi-arid savanna site of southern Africa in the presence and absence of grass competition. From the results, it can be concluded that 15% rainfall suppression has significant but transient effect on woody species growth and these effects are more pronounced at the establishment stage. Furthermore, the interaction of woody saplings and grasses shift from competitive to facilitative and vice versa in response to fluctuations in rainfall. Although rainfall is a key determinant of tree-grass ratios in savannas, other factors such as nutrient availability are also critical. In this regard, future studies need to test the effect of these two key resources i.e, rainfall and N in the presence and absence of grass competition in order to gain insights into tree-grass interactions in a changing environment.

Chapter 5

Effects of Nitrogen addition and rainfall suppression on *Vachellia karroo* growth under grass competition in a southern African savanna

This Chapter is based on:

Munyaradzi D. Shekede[1], Mhosisi Masocha[1] and Amon Murwira[1] (2018) Transient effects of nitrogen addition and rainfall suppression on *Vachellia karroo* growth under grass competition in a southern African savanna, Cogent Environmental Science, 4:1.

Abstract

Rainfall and nitrogen (N) are considered two most important resources limiting woody species recruitment and growth in savanna ecosystems. Yet, it is not clear how woody species, especially nitrogen-fixers will respond to the combined effect of increased N fertilisation and reduced rainfall amount in savannas in a globally changing environment. In this study, a field manipulative experiment was set up at Kyle Game Reserve in southern Zimbabwe to investigate the interaction effects of increased N deposition and reduced rainfall amount on the growth of *Vachellia karroo* saplings in the presence of grass competition. Rainout shelters were erected around experimental plants to mimic the projected decrease in rainfall in southern Africa savannas while N was added as ammonium nitrate over four growing seasons. The experiment uncovered significant but transient effects of rainfall suppression alone (F_1=5.171, P=0.031) and its interaction with N fertilisation (F_1=6.369, P=0.017) on the height of *V. karroo* saplings in the second growing season but not in the first, third and fourth season ($P > 0.05$). Specifically, rainfall suppression significantly reduced tree height while the interaction of fertilisation and rainfall suppression increased the stem height of the study species. In contrast, the interaction effects of N supply and rainfall suppression significantly (F_1=4.213, P=0.049) increased diameter growth of *V karroo* saplings during the first season but not thereafter. On the other hand, grass competition did not significantly influence the growth of our focal species either alone or in interaction with the main treatments though saplings growing in competition with grass had relatively higher growth than the control. Overall, results suggest that N fertilisation may cancel out the predicted negative effect of rainfall decrease on woody species growth thereby enabling the persistence of these species under global environmental changes.

5.1 Introduction

Rainfall and nitrogen (N) are known to limit woody species recruitment, productivity and diversity in savanna ecosystems (Scholes and Archer, 1997a, Vadigi and Ward, 2013, van der Waal et al., 2009c). Rainfall, in particular water, is considered the primary determinant of savanna structure (Sankaran et al., 2008) since water has a direct effect on the physiological processes of photosynthesis, respiration, and plant growth (Huston and Wolverton, 2009). Previous work has shown that maximum woody cover in savannas is regulated by mean annual rainfall (MAR). In semi-arid savannas receiving less than 650 mm of MAR water availability constrains woody cover resulting in a stable co-existence of trees and grasses (Sankaran et al., 2005b, Sankaran et al., 2008). In contrast, in humid savannas receiving ≥ 650 mm of MAR woody cover is not limited by water availability. As a result and in the absence of disturbances such as fire and herbivory, these humid savannas can easily transit into a woodland system hence they are considered unstable (Sankaran et al., 2005b).

With regard to plant nutrient requirements, N is the most important element required by plants in the largest amounts and savanna vegetation is no exception (Vitousek and Field, 1999, Chapin, 1980). However, in tropical soils where savannas are distributed, the availability of most essential plant nutrients including N is low due to the higher rates of nutrient loss and immobilization under warm wet conditions, as well as the old age of tropical soils (Huston and Wolverton, 2009). This picture is however changing in light of the observed global increase in N deposition (WallisDeVries and Bobbink, 2017, Valliere et al., 2017). For example, in semi-arid savannas of southern Africa, atmospheric N deposition has increased three to four fold between 1955 and 2003 (Scholes et al., 2003) and is likely to accelerate in future (Galloway et al., 2004, Sheffield and Wood, 2008a, Miyazaki et al., 2012). The key drivers of this increase include industrialisation (Conradie et al., 2016) and land use change (Galy-Lacaux and Delon, 2014, Adams et al., 2004). The observed changes in N deposition into savanna systems is occurring against the backdrop of a drying trend in rainfall patterns for southern Africa, (IPCC, 2007, Davis and Vincent, 2017, Hoerling et al., 2006, Hulme, 1996). While there are uncertainties in rainfall projections over southern Africa, decreases of between 10-30% are expected in this region (Serdeczny et al., 2017). Currently, not much is known about how the effect of the combined decrease in soil moisture availability and increased N deposition on tree-grass interactions in savannas. Yet, this knowledge is critical for savanna management in a changing world.

Although a number of observational and experimental studies investigated the effects of N addition on plant growth and competition interactions of woody and grassy species in savanna ecosystems, conflicting results have been reported. For instance, Sankaran et al., 2008 conducted a meta-analysis of determinants of woody cover in African savannas and found negative effects of increased soil N availability on woody cover owing to increased grass competitiveness. Similarly, in a semi-arid Mediterranean savanna, Trubat et al., (2011) reported a decrease in survival and performance of woody seedlings in a N addition study. In a bush encroached South African savanna, an experimental study by Kraaj and Ward (2006a) detected significant negative effects of N enrichment on woody species growth with amplified negative effects reported in plots with herbaceous competition. Overall, these studies demonstrate that an increase in soil available N enhances the growth of herbaceous plants resulting in the suppression of woody species recruitment and growth (Walker and Langridge, 1997, Moshe et al., 2000). This effect is amplified in N poor environments (Kraaij and Ward, 2006a, van der Waal et al., 2009c). Contrary to these studies, Ingestad (1980) reported that nitrogen enrichment stimulated woody species growth in a greenhouse experiment. Data from field experimental work in North American savannas by Siemann and Rodgers (2003) demonstrated that the growth of woody species increased with N supply. In addition, results from a meta-analysis by Xia and Wan (2008) concluded that N fertilisation stimulates woody plant growth with non-legumes being more sensitive to fertilisation than legumes.

In contrast to the above studies reporting either significant negative or positive effects of increasing N of woody species performance, Holdo (2013) did not detect significant effects of increasing N on the above ground biomass of a dominant woody species. Holdo’s experimental work was conducted in a South African savanna targeting a dominant woody species – *Colophospermum mopane*. Similarly, in a short-term greenhouse experiment, van Auken et al., (1985) previously found that N fertilisation did not significantly affect the growth of N fixer woody species –*Acacia smallii*. In addition, van der Waal et al., (2009c) and Mopipi et al. (2009a) showed that woody seedling growth was not significantly affected by N fertilisation in a nutrient poor semi-arid southern African savanna. Recently, in a study done in a southern African savanna, Barbosa et al., (2014a, 2014b) found out that N addition did not induce significant growth in above-ground biomass production of woody species regardless of whether they were N-fixers or non-fixers. Put together the above studies suggest that N fertilisation could have neutral, positive and negative effect on woody species recruitment. The lack of clear outcome on the effects of increased nitrogen on woody species requires further investigation especially in the context of increased N deposition in savannas across the globe.

So far most experimental studies performed to test the effects of changes in rainfall and N on woody species growth have manipulated either resource in isolation (Beier et al., 2012, Fensham et al., 2005a, Ludwig et al., 2001, Vadigi and Ward, 2013, van Auken et al., 1985, February et al., 2013, Berry and Kulmatiski, 2017). The few studies that have manipulated both resources have done so over short time scales (Barbosa et al., 2014a, Kraaij and Ward, 2006a, Ludwig et al., 2001, Trubat et al., 2011, van der Waal et al., 2009c, van Langevelde, 2003). In addition, some of the studies have manipulated these two resources in glass houses (van Auken et al., 1985). While glasshouse studies are important in eliminating confounding effects associated with field experiments they often fail to mimic the real world conditions (Limpens et al., 2012). In light of the shortcomings of these studies, our current understanding of the combined effects of key resources on woody species recruitment and growth remains limited (Higgins et al., 2007). This gap needs to be closed considering the observed widespread increases in nitrogen deposition and decreasing rainfall amounts are likely to significantly alter tree-grass interactions with far-reaching consequences on savanna structure and functioning.

To bridge this knowledge gap, a field experiment was conducted over four growing seasons to investigate the main and interaction effects of increasing N and reducing water availability on the growth of a common nitrogen fixer common in African savannas (*Vachellia karroo*). Fixed rainout shelters were erected around *V. karroo* saplings to reduce rainfall availability while N was added as ammonium nitrate in the presence and absence grass competition in a southern African savanna. The study tests the following hypotheses:

i. since tree growth is currently limited by rainfall, a 15% decrease will further constrain woody sapling growth.
ii. as grasses are more efficient in utilising resources in the upper soil layer than woody species, N addition will stimulate growth of grass species at the expense of woody species thereby amplifying their suppressive effects on woody species.
iii. N addition combined with rainfall reduction may dampen the competitive effects of grasses on woody species.

5.2 Materials and Methods

5.2.1 Study site

The experimental study was performed at Kyle Game Reserve located at 20°11’20.01″ of latitude and 30°58′58.17″ of longitude. The area is located at an average height of 1050m above sea level with a mean annual rainfall of 638 mm. The climate of the study area is semi-arid characterised by three seasons namely 1) hot and wet season from November to April, 2) cool and dry season between May and August and 3) hot and dry season between August and October (Shoko et al., 2015). Average maximum daily temperatures range from 21°C in June to 29°C in October while the average minimum daily temperatures range between 5°C and 17°C in July and January, respectively (Masocha and Dube, 2017). The study area is characterised by highly variable rainfall and frequent droughts which occur on annual to decadal scales (Shekede et al., 2016). Soils at the experimental site are mainly clays derived from the basement complex of banded ironstone and gold-belt schist (Wilson, 1964). Woody vegetation at the study site is dominated by *Dichrostachys cinerea, Vachellia karroo* and the invasive *Lantana camara (Masocha and Skidmore, 2011).* The herbaceous layer at the study site mainly consists of *Hyparrhenia filipendula* and *Hyperthelia dissoluta* (Vincent and Thomas, 1960). Key animal species at the study site include *Phacochoerus africanus, Syncerus caffer, Ceratotherium simum, Aepyceros melampus and Giraffa cameleopardalis.* Our species of interest for this study was *V. karroo* which constitutes a significant proportion of vegetation cover in the Game Reserve and is one of the key encroacher species in southern African savannas (O'Connor et al., 2014).

5.2.2 Selection of experimental plants

Prior to setting up the field experiment, five candidate sites dominated by *V. karroo* adult trees interspersed with a continuous herbaceous layer were identified. At each candidate site measuring approximately 100 m by 100 m, 1-m belt transects were laid out in October 2012. Transects were placed ten metres apart. In each transect, three observers identified and counted the number of *V. karroo* seedling and saplings considered to belong to the same age cohort on the basis of similarity in height. An individual was classified as a seedling if it was less than 5 cm in height whereas those above 5 cm and with a diameter at the base greater than 1 cm were classified as saplings. The field experiment targeted seedlings or saplings because these growth stages experience intense competition with grasses whose outcome can be mediated by resource availability and environmental changes leading to either woody species recruitment success or failure. Due to the failure to identify sufficient number of seedlings (> 50 individuals at each candidate site), a decision was made to use *V. karroo* saplings as the experimental units. One site with more than 50 *A. karroo* saplings was randomly chosen to guarantee sufficient number of replicates for the experiment. The site was fenced off to exclude herbivory by small and large mammals.

Prior to starting the experiment, each *V. karroo* sapling identified was assigned a unique label and measured for stem height, basal stem diameter and number of secondary branches. Then, a total of 48 saplings that were similar in size located at least 2 m from the edge of fence were selected at random to minimize the influence of treatments among plots. To reduce the confounding effect of size, one-way analysis of variance (ANOVA) was used to test and confirm that there were no significant differences in sapling basal diameter and height. ANOVA results indicated that there were no significant differences in the stem basal diameter

(F_{40}=0.402, P=0.895) as well as sapling height (F_{40}=0.768, P=0.617) at the start of the experiment. A 1-m by 1-m plot with the focal sapling centrally located was established around each selected sapling before random assignment of treatments.

5.2.3 Experimental design

To investigate how nitrogen (N) fertilisation and changes in rainfall reduction affect the growth of *Vachellia karroo*, a field experiment in which N and rainfall amount were manipulated in the presence and absence of grass competition was set up. The field experiment consisted of three main treatments each with two levels, that is 1) rainfall suppression versus natural rain; 2) nitrogen addition versus no nitrogen; and 3) grass competition versus no grass competition. The experiment followed a fully crossed design to yield a total of eight different treatment combinations:

(1) adding N in the presence of competition from herbaceous vegetation;

(2) adding N in the absence of competition from herbaceous vegetation;

(3) reducing rainfall amount by 15% in the presence of competition from herbaceous vegetation;

(4) reducing rainfall amount by 15% in the absence of competition from herbaceous vegetation;

(5) herbaceous vegetation left intact to allow competition;

(6) simultaneously adding N and reducing rainfall in the absence of competition from herbaceous vegetation;

(7) simultaneously adding N and reducing rainfall in the presence of competition from herbaceous vegetation; and the

(8) control in which no N was added, rainfall was not reduced and herbaceous vegetation was removed.

5.2.4 Treatments

Each treatment combination was replicated six times to yield a total of 48 experimental units at the start of the experiment. N was applied as a top dressing at a rate of 4 grams of N m^{-2} at the start of the rainfall season in October. Nitrogen fertilizer was added in the form of ammonium nitrate (NH_4NO_3) granules evenly sprinkled within the plot by hand. This application rate is 3 times the N deposition rates projected for southern Africa for the 2050s (Phoenix et al., 2006).

To mimic IPCC (2007) rainfall projections for southern Africa, rainfall was reduced by 15%). This was achieved by constructing a fixed-location rainout shelters around each 1-m by 1-m plot experimental plot following the design used by Yahdjian and Sala (2002). The rainout shelter with had arcyllic bands on the roof designed to direct excess rainfall to a storage container that was emptied after rainfall event. The sides of the rainout shelter were left open to allow free air circulation and to minimize the confounding effects of temperature and humidity (Fiala et al., 2009). The rainout shelter was maintained throughout the duration of the experiment. Control plants had no rainout shelters and thus received normal rainfall. During the experimental period, the amount of rainfall suppressed was variable with as little as 50 mm (for a rainfall total = 337 mm) in 2012 to as much as 125 mm in 2014 (for a rainfall total 832 mm)

Competition between *V. karroo* saplings and herbaceous vegetation was manipulated by clipping to ground level all above-ground herbaceous biomass present in control plots at the start of the experiment and monthly thereafter. The herbaceous competition treatment included both perennials and annuals. However, some 11 saplings died during the course of the experiment resulting in an unequal number of experimental units across treatments. Unlike, some woody species that died completely during the course of experiment, herbaceous plants especially perennials, recovered during the wet season after parts of the plants died off during the dry season. The experiment ran from October 2012 to October 2016.

5.2.5 Monitoring *V. karroo* sapling growth

V. karroo saplings were monitored from October 2012 to September 2016. To quantify the treatment effects on *V. karroo* growth, basal diameter and stem height were measured on each individual at the end of every month. Here, only the results for the month of May of each of the four growing season are presented as these represent the growth accumulated during the growing season. At the study site, the growing season stretches from November to April. Basal diameter was measured using a veneer caliper at a height of 2 cm from the ground level. Sapling height was measured using a tape measure and height was considered as the highest point of the plant from the ground surface.

5.2.6 Statistical Analysis

Factorial ANOVA was used to test whether the means differed significantly among the eight treatments. Post-hoc multiple comparisons based on the Fischer's LSD test were done when the null hypothesis that the means were the same was rejected by ANOVA. Statistical analysis was done separately for stem height and basal diameter. Prior to statistical analyses data on stem height and diameter data were log transformed and square rooted, respectively, to reduce skewness. The data were then tested for normality using Shapiro-Wilk's test. All statistical analyses were performed in STATISTICA version 10 (StatSoft,Inc., Tusla,Oklahoma,USA) and the results are reported for four growing seasons separately. The seasonal approach was adopted in this study to reduce the confounding effects of negative growth that may occur during dry season.

5.3 RESULTS

5.3.1 Effects of N addition, rainfall suppression and grass competition on the variation in height of *V. karroo* saplings

Figure 5.1 illustrates the effects of N fertilisation, rainfall suppression and grass competition as well as their interactions on height increment of *V. karroo* saplings across four growing seasons. We observe that the height of *V. karroo* saplings exposed to different treatments generally increased across the four growing seasons. N fertilisation in the absence of grass competition had negative but non-significant effect on the growth of *V. karroo* saplings across the four seasons (Table 5-1). In contrast, N fertilisation in the presence of grass competition resulted in larger height increment than fertilisation alone. However, the height differences in plots with and without grass completion were not statistically significant across the duration of the experiment (Table 5-1).

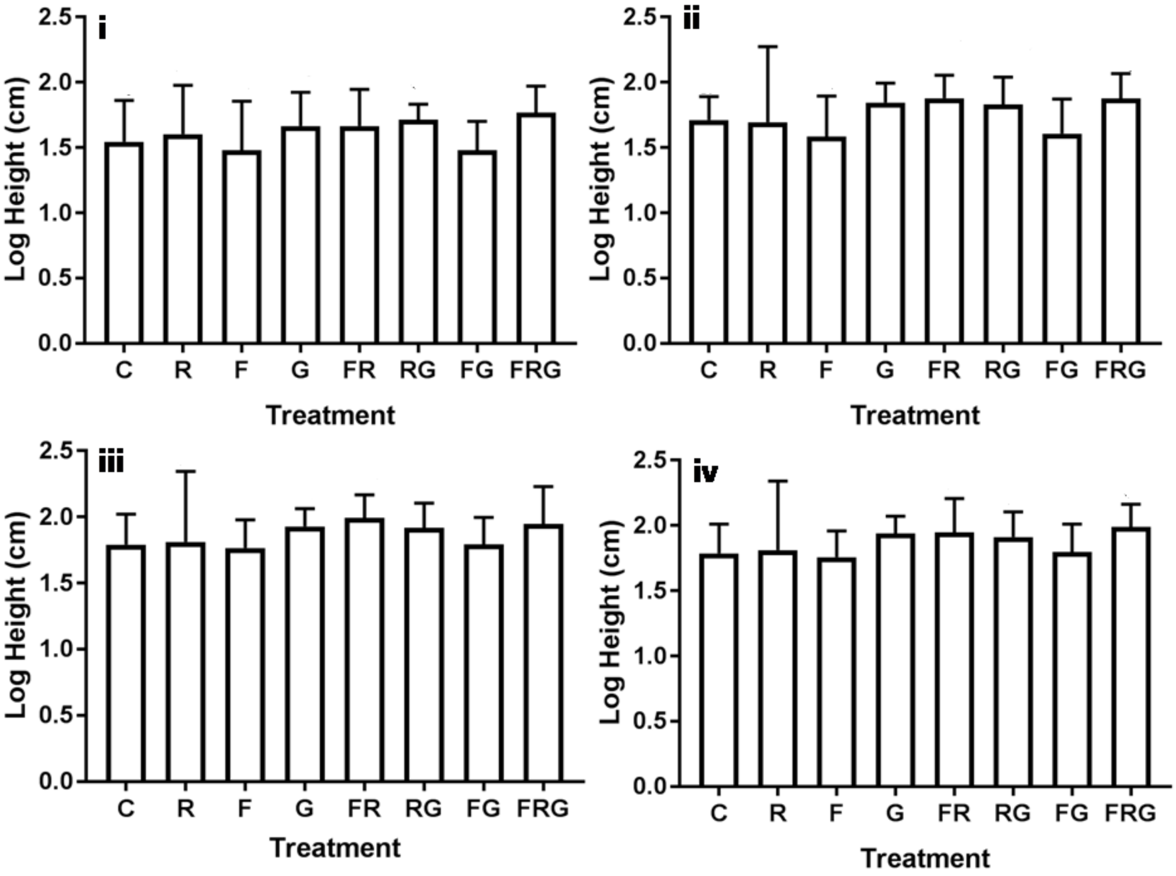

Figure 5.1: Effects of N fertilisation, rainfall suppression and grass competition on the mean log height of V. karroo saplings after i) first growing season, ii) second growing season, iii) third growing season and iv) fourth growing season C=control, F=N addition, G= Grass competition and R=Rainfall suppression. Error plots represent log mean ±95% Confidence Interval

.

Results for ANOVA illustrate that rainfall suppression alone did not have significant effects on the height of *V. karroo* saplings across all growing seasons except in the second growing season (Table 5-1). Specifically, in the second season, rainfall suppression significantly and positively influenced the stem height of *V. karroo* saplings with plants grown under rainfall suppression having a greater stem height (log mean 1.81±0.12cm (Standard Error) than those in the control (log mean 1.79±0.08 cm). Nonetheless, the effects of these treatments are not detectable at the end of the third and fourth growing season (Table 5-1). A comparison of growth patterns of *V. karroo* saplings illustrates that rainfall suppression induced more height increment in the presence of grass competition than without. In particular, plants exposed to rainfall suppression in the presence of grass competition increased in height 6% more than those that were exposed to rainfall suppression alone.

Table 5-1: Effects of N addition, Rainfall suppression, grass competition and their interaction on height increment of *V. karroo* saplings

	Start of Experiment		1st Season		2nd Season		3rd Season		4th Season	
Effect	F	P	F	P	F	P	F	P	F	P
Intercept	9923.54	0.000	1993.85	0.000	3586.89	0.000	4811.70	0.000	4816.85	0.000
Fertilizer (F)	0.110	0.742	0.214	0.647	0.333	0.568	0.052	0.821	0.045	0.833
Rainfall (R)	3.638	0.066	4.012	0.055	5.171	**0.031**	3.306	0.079	3.142	0.087
Grass (G)	0.010	0.922	0.210	0.650	1.576	0.219	2.192	0.149	2.404	0.132
F*R	0.273	0.605	1.609	0.215	6.369	**0.017**	3.006	0.094	3.216	0.083
F*G	2.873	0.101	1.342	0.256	1.081	0.307	0.614	0.439	0.601	0.444
R*G	0.010	0.921	0.155	0.696	0.005	0.946	0.002	0.964	0.043	0.837
F*R*G	0.002	0.963	0.104	0.749	0.008	0.931	0.060	0.808	0.071	0.792

The interactive effects N fertilisation and rainfall suppression had significant effects on the height of *V. karroo* saplings only in the second season. However, these effects were more enhanced in plots with grass competition than without (Figure 5.1 and Table 5-1). Table 5-2 shows the results of the Posthoc analysis performed to test which means significantly differ from each other.

Table 5-2: Results of the Posthoc analysis based on the Least Significant Difference test on tree height growth in the second season. The black dots indicate treatments that significantly differed from each other

	C	G	Rl	F	R &G	F R	F G	F R G
C								
G								
R								
F		●						
RG				●				
F R				●				
F & G		●			●	●		
F, R G				●		●		

5.3.2 Effects of N addition, rainfall suppression and grass completion on diameter increment of *V. karroo* saplings.

The variations in diameter growth of *V. karroo* saplings exposed to N addition, rainfall suppression, grass competition and their interactions are shown in Figure 5.2. Results illustrate that, similar to height growth patterns, N addition alone and in combination with grass competition did not significantly affect the diameter of *V karroo* saplings though plants subjected to N addition had larger diameter than those under a combination of fertilisation and grass competition (Table 5-2)

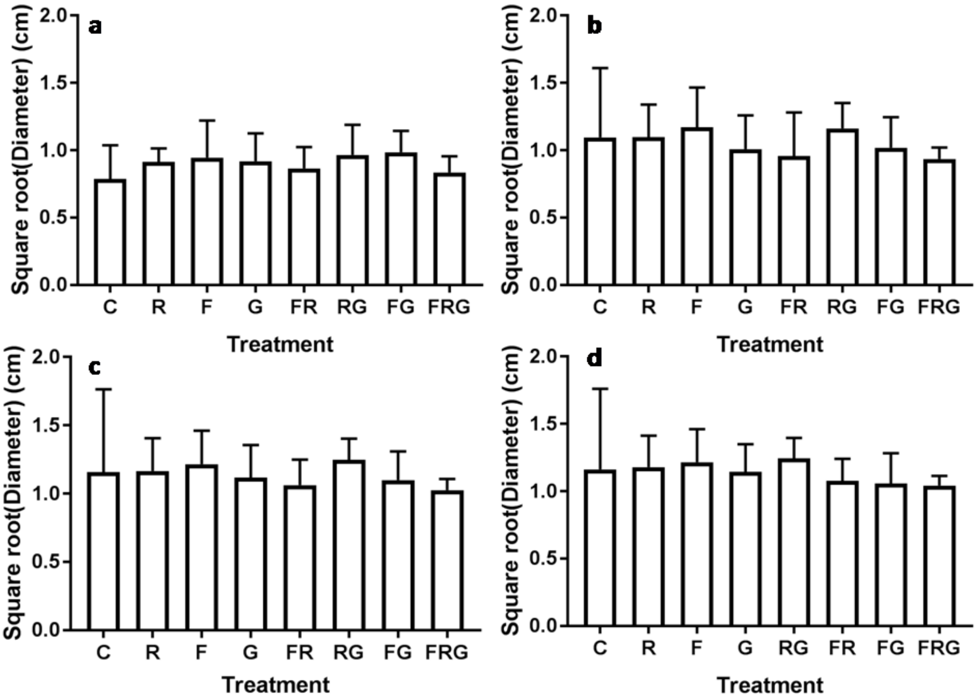

Figure 5.2: Effects of N fertilisation, rainfall suppression and grass competition on diameter of *V. karroo* saplings after a) first growing season, b) second growing season, c) third growing season and d) fourth growing season. C=control, F=N addition, G= Grass competition and R=Rainfall suppression. Error plots represent mean ±CI.

Furthermore, we observe rainfall suppression alone and in combination with grass competition did not appear to significantly affect the diameter of *V.karoo* saplings. A comparison of the growth patterns of these plants illustrate that saplings growing under rainfall suppression had smaller diameter than those exposed to a combination of rainfall suppression and grass competition. We also observe that by the end of the first growing season, the interaction of rainfall suppression and N addition is the only treatment that negatively and significantly affected diameter of *V. karroo* saplings. Specifically, the diameter of *V. karroo* saplings exposed to the interaction of rainfall suppression and N treatment had significantly smaller diameter (1.14±0.12cm) than the control (1.24±0.19cm). Moreso, we did not observe any significant effects of main treatments or their interactions thereafter (Table 5-3).

Table 5-3: Effects of N addition, Rainfall suppression, grass competition and their interaction on stem diameter growth of V. karroo saplings

	Start of experiment		1st growing season		2nd growing season		3rd growing season		4th growing season	
Effect	F	P	F	P	F	P	F	P	F	P
Intercept	374.27	0.000	331.60	0.000	290.20	0.000	383.40	0.000	404.8	0.000
Fertilizer (F)	0.202	0.656	0.022	0.885	1.298	0.264	1.694	0.203	2.331	0.138
Rainfall (R)	0.965	0.334	0.094	0.762	0.305	0.585	0.179	0.675	0.051	0.822
Grass (G)	0.017	0.898	1.264	0.270	0.571	0.456	0.194	0.662	0.378	0.543
F*R	0.137	0.714	4.213	0.049	3.202	0.084	2.414	0.131	1.510	0.229
F*G	0.340	0.565	0.812	0.375	0.386	0.539	0.589	0.449	0.886	0.355
R*G	0.721	0.403	0.463	0.501	1.075	0.308	0.699	0.410	0.737	0.398
F*R*G	0.157	0.695	0.007	0.934	0.028	0.867	0.054	0.819	0.007	0.936

5.4 Discussion

The aim of this study was to test whether N fertilisation and rainfall suppression mediated by grass competition have significant effects on the growth of *V. karroo* saplings growing in a semi-arid savanna ecosystem. Our results indicate that interactions between N fertilisation and rainfall suppression have significant but transient effects on the growth of woody saplings. In addition, rainfall suppression significantly reduced height but not diameter of our focal species. On the other hand, grass competition did not significantly influence the growth of our focal species either alone or in interaction with the main treatments. However, saplings growing in competition with grass had relatively higher growth than the control.

5.4.1 Effects of Nitrogen on V. karroo sapling growth

Results of our short-term experiment indicate that N fertilisation alone had negative but non-significant effects on the growth of *V. karroo,* a nitrogen fixer. This is contrary to the expectation that nitrogen addition would significantly increase the growth of our focal species based on the premise that the ready availability of N would result in the reallocation of energy from N fixation to other processes such as growth. Results of this study are consistent with previous studies that observed a 20% reduction in woody species growth as a result of N addition (Schuster and Dukes, 2017). Similar studies (Mopipi et al., 2009b, Van Der Waal et al., 2009a, Xia and Wan, 2008) found no significant effects of N addition on the growth of woody seedlings in semi-arid savannas. In recent studies, Barbosa et al., (2014a, 2014b) found out that N addition did not induce significant growth in above-ground biomass production of woody species regardless of whether they were N-fixers or non-fixers in a southern African savanna. Indeed, the growth of leguminous woody species especially

Vachellia can be insensitive to N addition but may respond positively to other mineral nutrients (van Auken et al., 1985).

Although the mechanism explaining the growth pattern found in this study is not clear, we speculate that under increased N conditions, other factors such as water and Phosphorous may be limiting resulting in investment of energy towards the root system of the plants to increase water and nutrient foraging capability (Mokany et al., 2006, Vitousek et al., 2002, Xia and Wan, 2008). These results are confirmed by previous research that have documented negative relationship between soil available N and woody biomass (Sankaran et al., 2008, Walker and Langridge, 1997). The negative effects of increased N availability on woody biomass growth have been explained through competition-based mechanism. Through this mechanism, herbaceous species are hypothesised to directly pre-empt N or indirectly reduce critical resources such as light or water available to woody species as a result of enhanced herbaceous species growth (Kraaij and Ward, 2006a, Sankaran et al., 2008). However, in plots with N addition alone, we removed grass competition thereby ruling out the competitive effects of grasses on *V. karroo* saplings.

Nitrogen fertilization led to the increase in the basal diameter of *V. karroo* species, though the effects were not significant. Our results are confirmed by previous studies that observed investments in basal diameter under conditions of increased nutrient availability (Vadigi and Ward, 2013). Conversely, nitrogen addition had negative effects on the stem height of our focal species. These two contrasting results of the response of *V. karroo* saplings to increased nitrogen availability could be reflecting unique and time-variant resource allocation strategy aligned to addressing limitations to plant growth imposed by the environment. Previous studies have demonstrated a change in biomass allocation to shoots or storage organs in response to increased nitrogen availability (Ingestad and Agren, 1991, Miranda et al., 2014, Poorter and Nagel, 2000, Poorter et al., 2012). Our results fit well with the optimal partitioning models which suggest that plants act in response to environmental variation through partitioning biomass among organs to optimize resource acquisition and maximize growth (McCarthy and Enquist, 2007).

5.4.2 Effects of rainfall suppression on the growth of *Vachellia karroo* saplings

Contrary to hypothesis 1 that expected rainfall suppression to reduce the growth of *V. karroo* saplings result from this study indicate that that rainfall suppression significantly increased height but not diameter of *V. karroo* saplings in the second season after the start of the experiment. Specifically, saplings growing under 15% rainfall suppression had a larger mean height but smaller mean diameter than the control suggesting some compensatory behaviour in the growth patterns of our focal species. A possible mechanism explaining the larger height increment in the second season of saplings under rainfall suppression compared with the control could be increased water use efficiency. Recent studies have shown that increased water use efficiency of woody species associated with increasing aridity helps in overcoming precipitation driven constraints (Devine et al., 2017a). Consequently, plants growing in environments with moderate reduction in precipitation can exhibit similar growth patterns as the control as long as the reduction in precipitation does not result in severe moisture stress (Padilla et al., 2009, Poorter et al., 2012). In fact, aridity is cited as a key factor in explaining variance in Nitrogen-fixer abundance across the globe (Pellegrini et al., 2016). Our results are also consistent with findings by February et al., (2013) who observed that woody species establishment was more pronounced during periods of short-term droughts when grass competition is reduced. Overall, our finding implies the possibility of persistence of Nitrogen fixing woody plants in a drying environment that is anticipated in southern African savannas in future.

5.4.3 Interactive effects of rainfall suppression and Nitrogen addition on *Vachellia karroo* saplings' growth

Results of this study have shown that N fertilisation coupled with rainfall suppression significantly and positively increased sapling height and diameter of *V. karroo* saplings. This suggests that the potential negative effects of relative moisture stress imposed on *V. karroo* saplings' growth could be counteracted by Nitrogen fertilisation. In fact, N fertilization under reduced rainfall could increase plant tolerance to soil moisture stress (Kinugasa et al., 2012) through, for example, increasing below ground biomass (Van den Driessche, 1992). In addition, studies elsewhere have shown that N-fixing plants are capable of sustaining high foliar N concentrations leading to efficient water use (Adams et al., 2016). This may result in larger growth rates for sapling growing in water suppressed environment compared to plants growing under natural rainfall. Our results are confirmed by previous research that observed significant interactive effects of nutrient addition and water manipulation on woody seedling growth suggesting mediating effect of rainfall reduction on the growth of *V. karroo* saplings (Adams et al., 2016).

5.4.4 Effect of grass competition on *V. karroo* sapling growth

Contrary to findings from previous studies, our results showed that grass competition alone and in interaction with either N fertilisation or rainfall suppression did not have significant effects on the growth (diameter and height increment) of *V. karroo* saplings. Similar studies have observed the suppressive effects of grass competition on woody species especially at the early stages of growth when grasses and woody species have intense competition for resources in the upper layers as predicted by Walter's competition model (Cramer et al., 2007, Knoop and Walker, 1985, Vadigi and Ward, 2013, Van Der Waal et al., 2009a). However, it is not unusual to observe lack of suppressive effects of grasses on woody species especially N-fixers as previously documented by (O'Connor, 1995). In fact, several ecological studies have emphasised the increasing importance of facilitation over competition under conditions of increased abiotic stress (Callaway, 2007, Dohn et al., 2013, He et al., 2013, Maestre et al., 2009); with the largest facilitative effects being realised at intermediate stressful conditions (Holmgren and Scheffer, 2010). A recent study on understanding tree-grass interactions along a rainfall gradient by Mazía et al., (2016) has shown that facilitation could even extend up to 1800 mm. In our case a 15% reduction in rainfall might have been marginally stressful and thus, enhanced facilitation between grasses and woody saplings for Nitrogen since N-fixers have been shown to transfer fixed N to non-legume species (Sierra and Nygren, 2006, Zhang et al., 2016). Our study could be providing new insights into the role of facilitation in shaping plant communities even under unstressful conditions. In fact, our study could be confirming that facilitation does not necessarily need to occur under severe environments as previously thought.

The lack of significant interactive effects of N addition and grass competition on *V. karroo* saplings could also suggest the scale dependence nature of the growth of our experimental plants. Previous studies have demonstrated that plants respond differently to coarse versus fine-scale nutrient application (Hutchings et al. 2003, Birch and Hutchings 1994; Fransen et al. 1998, Kume *et al.* 2006, van der Waal et.al., 2010). For the N addition and grass competition treatment, fertiliser was sprinkled by hand thereby making it available as scattered grains instead of patches or heaps inside the experimental plots. Consequently, we speculate that grasses might have been more efficient in exploiting fertilizer applied at fine scale application than woody species thereby lowering growth rate of saplings exposed to N addition in the presence of grass competition than N addition alone. The the overall lack of significant interactive effects of rainfall suppression and N addition could also be explained by the slow rate of downward movement of N to the root zone as a result of relatively low amounts of rainfall.

An important finding of this study is that while rainfall suppression and its interaction with N addition significantly affected the growth of *V. karroo* saplings, these effects may be transient. In fact, results indicate that 15% rainfall suppression alone and its interaction with fertilizer addition had significant effects on the diameter of our focal species only in the second growing season. Similarly, the interaction of rainfall suppression and N addition only had significant effect on the diameter of *V. karroo* saplings in the first growing season but could not be detected thereafter. To the best of our knowledge, our study is among the few that have reported transient effects of rainfall suppression and N addition woody nitrogen fixers.

The novelty of this study lies in manipulating rainfall, nitrogen and grass competition under field conditions to test whether these factors significantly influence the growth of *V. karroo* saplings in a semi-arid savanna. Previous studies on effects on nitrogen deposition have either been carried out on relatively short time scales (Barbosa et al., 2014a, Holdo, 2013, Kraaij and Ward, 2006a, Mopipi et al., 2009b, Van Der Waal et al., 2009a) or were performed in green houses and thus, may not provide useful insights into the response of savanna woody species to changes in key resources. This therefore underscores the importance of long term studies in understanding the effects of global nutrient enrichment and changes in rainfall patterns on savanna ecosystem structure and function over longer time scales (Bhadouria et al., 2016). In addition, our study is among a few that has manipulated key resources limiting growth of key woody species in the presence and absence of grass competition. We assert that studies testing interactive effects of key resources are critical to the understanding of the combined effects of global environmental change and herbaceous competition on tree-grass ratios in tropical ecosystems.

While useful insights have been gained from assessing the effects of key limiting resources and grass competition in savannas based on a leguminous woody species, it is important that future work focus on the response of multiple functional species typical of savannas. This is especially important considering that non-leguminous plant species are incapable of fixing nitrogen and may thus; respond differently to un/availability of key resources. For instance, it has often been hypothesised that nitrogen-fixer plants may lose their comparative advantage over non-nitrogen fixer plants in the event of increased nitrogen deposition. In addition, nitrogen fixers are also predicted to increase their water use efficiency under a drying climate as a result of increase in carbon fertilisation. It may therefore be important to manipulate multiple resources on several plant species with different functional traits in order to enhance our understanding of tree-grass interactions in savannas that are undergoing transformation due to global environmental changes.

6. Conclusion

The objective of this experimental study was to assess the interactive effects of rainfall decline and N availability in the presence and absence of herbaceous competition on the growth of *V. karroo* saplings in semi-arid savannas. Results show that, similar to rainfall suppression alone (Chapter 4), N addition and its interaction with rainfall suppression had significant positive but transient effects on the growth of *V. karroo* saplings. Moreover, grass competition did not significantly affect the growth of *V. karroo* saplings. Combined, results suggest that the negative effect of rainfall suppression could be cancelled out by nitrogen fertilisation. Although we have increased our knowledge on the potential tree-grass interactions under a changing environment, more insights could be got through modelling future potential distribution of the target species. In this regard, coupling of species distribution models and future climate data from Global Circulation Models could help in tracking potential changes in woody species distribution as a first towards informing managemenent of savanna ecosystems.

Chapter 6

The bioclimatically suitable habitat of *V. karroo* is likely to increase in Zimbabwean savannas (southern Africa) under a changing climate

This Chapter is based on:

Shekede, M.D., Murwira, A. Masocha, M and Gwitira, I., 2018. Spatial distribution of Vachellia karroo in Zimbabwean savannas (southern Africa) under a changing climate, *Ecological Research Journal*, DOI: 10.1007/s11284-018-1636-7

Abstract

Climate change projections in southern Africa show a drier and a warmer future climate. It is not yet clear how these changes are going to affect the suitable habitat of woody encroacher woody species in southern African savannas. Maximum Entropy niche modelling technique was used to test the extent to which climate change is likely to affect the suitable habitat of *Vachellia karroo* in Zimbabwe based on six Global Climate Models (GCMs) from Coupled Model Intercomparison Project Phase 5 (CMIP5) and two Representative Concentration Pathways (RCPs) for the 2070s. An overlay analysis was then performed in a Geographic Information System based on the current and future bioclimatically suitable areas for the respective GCMs and RCPs. This was done to determine the potential effect of climate change on the focal species. Results show that temperature related variables are more important in explaining the spatial distribution of *V. karroo* than precipitation related variables. In addition, results indicate an overall increase in the modelled suitable habitat for *V. karroo* by the 2070s across the GCMs and RCPs considered in this study. Specifically, the suitable habitat of *V. Karroo* is projected to increase by a maximum of 57,594 km^2 signifying a 69% increase from the current suitable habitat (83,674 Km^2). The suitable areas are projected to increase in eastern, western and south eastern parts of Zimbabwe. These results imply that improved understanding of the response of woody species to a changing climate is important for managing woody encroachment in savanna ecosystems.

6.1 Introduction

Climate change could have profound effects on ecosystem processes by affecting the spatial configuration of ecosystems especially in arid to semi arid savannas where rainfall is currently a limiting factor (Sankaran et al., 2004, Scholes and Archer, 1997a, Scholes, 2015). In southern African savanna ecosystems, woody encroachment i.e., the increase in woody species density and cover in former grass dominated ecosystems is hypothesised to increase under a drying climate (Angassa, 2014, Midgley and Bond, 2015). However, the effects of climate change on the actual extent and rate of woody encroachment particularly for key savanna species are not well documented (O'Connor et al., 2014b). Thus, generation of knowledge on the potential effects of climate change on the spatial distribution of key savanna species is critical.

Although the number of studies that have assessed climate change effects on terrestrial ecosystems have increased, the majority have focused on large scale biome shifts in woody vegetation systems (Delire et al., 2008, Zelazowski et al., 2011, Dhlamini, 2010, Rutherford et al., 2000). These biome scale studies have advanced our knowledge of potential climate induced vegetation shifts, but little is known about the response of specific woody species to climate change in southern African savannas. Specifically, a review of literature shows that few studies have focused on specific species that are hypothesised to become significant under a changed climate at smaller spatial scales (Tews et al., 2006, Tews and Jeltsch, 2004 , Midgley and Thuiller, 2011), particularly in southern Africa. Yet spatial shifts i.e., expansion or contraction in the habitat of specific woody species resulting from climate change, can have observable effects at fine spatial scales (Gwitira et al., 2014). Thus, modelling of species-specific response to a changing climate at fine scale is critical for informing targeted management of ecosystems (Oldeland et al., 2010). In fact, an understanding of how key woody species respond to a changed climate is therefore important for the strategic management of savanna ecosystems.

Understanding the potential impacts of climate change on ecosystems has generally benefited from advances in species distribution models (SDMs) coupled with the development of Global Circulation models (GCMs) (hereinafter climate models) whose projections help with tracking potential spatial shifts in species distribution including woody species. For southern Africa, climate model projections indicate a general decrease in precipitation coupled with increased spatial and temporal variability and an increase in the frequency of occurrence of extreme events such as droughts (IPCC, 2014a). Temperatures are projected to exceed the 1981-2000 baseline by between 3.4°C and 4.2°C towards the end of the 21st century (Moise and Hudson, 2008). These projected changes in climate could have important implications on the persistence of woody species in savannas. Consequently, studies focused on understanding the distribution and dynamics of woody species using projected climate change scenarios could be useful in generating important information for ecosystem management.

This study modelled the potential effect of projected climate change on the distribution of *Vachellia karroo,* a key woody species in the Southern African arid and semi-arid savannas. The study tested whether and in what direction the bioclimatically suitable area of *V. karroo* is likely to shift in response to projected changes in climate.

6.2 Materials and Methods

6.2.1 Study area

The study was carried out in Zimbabwe, located in southern Africa between latitudes 15°30″ and 22°30″S and between longitudes 25°00″ and 33°10E″. Zimbabwe lies predominantly in the southern African savanna vegetation zone which is dominated by dry Miombo, Mopane as well as Terminalia/Combretum woodlands. Other vegetation types include serpentine grasslands mostly found along the Great Dyke and the Montane forest interspersed amongst high-altitude grasslands in the eastern parts of the country (Mapaura and Timberlake, 2004). Annual rainfall ranges from below 400mm in the southern, western and north-western parts of the country to above 1000mm in the central and eastern parts of the country (Figure 1). Zimbabwe experiences mean annual temperature of 18°C in the eastern highlands and about 23°C in the low lying areas. Temperature can range from a minimum of 15°C in the winter month of July to a high of 24°C in November. The country has four seasons i.e., cool dry season (mid-May to August), hot season (September to mid-November), main rainy season (mid-November to mid-March) and post rainy season (mid-March to mid-May). Rainfall is highly variable in space and time with frequent droughts being common. These droughts vary in duration, intensity and spatial extent.

6.2.2 Data on study species

Data on the spatial distribution of *Vachellia karroo (Hayne) Banfi & Galasso* were obtained from the National Herbarium and Botanic Garden offices in Harare, Zimbabwe. These data were collected from quarter grids (~28 km x 28 km). Complementary locational data on *V. karroo* were extracted from a monogram by Barnes et al., (1996). The data are based on the location of representative specimens collected throughout southern Africa, including Zimbabwe. A total of 70 occurrence records of *V. karroo* were obtained from these two sources. The selection of *V. karroo* as the study species is based on literature (Kgosikoma and Mogotsi, 2013, Moleele, 2002, O'Connor et al., 2014b, Wigley et al., 2010a, Katjiua and Ward, 2006, Barnes et al., 1996), which identifies the woody species as widespread in southern African savannas.

6.2.3 Current and Future climate data

In order to model the response of *V. karroo* to a future climate, current and future climate data were downloaded from the world climate database (Hijmans et al., 2005), http:/worldclim.org) and the Climate Change, Agriculture and Food Security climate data portal (http://www.ccafs-climate.org/. The current climate data were derived from interpolations of observed data representative of 1960-1990 from the Coupled Model Intercomparison Project Phase 5 (CMIP5). Table 6-1 summarises the climate dataset representative of the 2070s used in this study.

Table 6-1: The six GCMs used for modelling the response of V. karroo to projected changes in climate

Climate Model	Abbreviation Adopted in this study
Beijing Climate Centre Climate System Model (BCC-CSM 1.1)	BC
Commonwealth Scientific and Industrial Research Organisation (CSIRO MK 3.6.0)	CS
National Centre for Meteorological Research (CNRM-CM5)	CN
Goddard Institute for Space Science (GISS)	GS
Hadley Centre Model (HadGEM2-ES)	HE
The Norwegian Earth System Model (NorESM1M)	NO

Bioclimatic data (Nix, 1986) were then derived from these GCMs (Table 6-2). The bioclimatic data had a spatial resolution of 30 arc-second resolution grid (~1km^2) and were based on two extreme representative concentration pathways namely RCP 2.6 and RCP 8.5 as comparative future scenarios for the 2070s (Moss et al., 2008). The RCP2.6 represents the mitigation scenario leading to a very low forcing level of a maximum of 3 W/m^2. In contrast, RCP 8.5 projects a rising radiative forcing pathway leading to 8.5 W/m^2 by 2100 (van Vuuren et al., 2011). Six GCMs and two RCPs were selected in order to capture uncertainties related with impacts and adaptation planning for savanna ecosystem.

Table 6-2: The 19 bioclimatic variables used in species distribution modelling

Bioclimatic variable	Description
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range
BIO3	Isothermality
BIO4	Temperature Seasonality
BIO5	Maximum Temperature of Warmest
BIO6	Minimum Temperature of Coldest Month
BIO7	Temperature Annual Range
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality
BIO16	Precipitation of Wettest Quarter
BIO 17	Precipitation of Driest Quarter
BIO 18	Precipitation of Warmest Quarter
BIO 19	Precipitation of Coldest Quarter

Average rainfall and temperature across all the six GCMs and two RCPs of the 2070s were calculated based on the current and projected rainfall (BIO12) and temperature (BIO1). Rainfall and temperature anomalies were then calculated by finding the difference between the future average temperature and rainfall for the 2070s and current climate. Positive and negative values on the anomaly maps indicate and decrease in the two climatic variables, respectively.

6.2.4 Modelling the spatial distribution of *V. karroo*

6.2.4.1 Tests for Collinearity

Prior to modelling the distribution of *V. karroo*, bioclimatic data were first tested for collinearity i.e., strong correlation between predictor variables, among the nineteen climatic variables using the Variance Inflation factors (VIF) (Akinwande et al., 2015, Marquardt, 1970). Multicollinearity among bioclimatic variables can result in over-fitting of models in species distribution modelling (Pradhan, 2016). In Species Distribution Modelling, VIFs provide an estimate of how much of a predictor’s variability is explained by the rest of the predictors in the model due to correlation among the regressors (Craney and Surles, 2002).

VIF stepwise function accessible through the Uncertainty Analysis for Species Distribution Models (USDM) in R (Naimi, 2014) was used to iteratively remove collinearity among bioclimatic variables by calculating VIF of variables against each other. Through this analysis, a variable is removed when its VIF is regarded as being too large. In this study, a cutoff value of 10 was adopted to determine collinearity based on typical suggestions from literature (Craney and Surles, 2002, Lubestzky-Vilnai et al., 2013, Stine, 1995). The following bioclimatic variables were highly correlated and were thus excluded in the species distribution modelling: BIO1, BIO5, BIO8, BIO10, BIO11 and BIO17. After removing correlated bioclimatic variables, the spatial distribution of *V. karroo* was modelled under both the current and future climates based on the 2.6W/M^2 and 8.5 W/M^2 RCPs for each of the six GCMs used in this study. The final modelling did not include altitude because it is often considered bioclimatically irrelevant for climate change studies (Dhlamini, 2010).

6.2.4.2 Predicting V. *karroo* distribution

Maximum Entropy (MAXENT) ecological niche modeling technique (Phillips et al., 2006) was adopted to model the current and future (2070s) spatial distribution of *V. karroo* species based on six climate models and two RCPs i.e., RCP2.6 W/m^2 and RCP 8.5 W/m^2. MAXENT is a presence only species distribution modelling technique used to estimate a species' niche in geographic space through correlating observed occurrences to bioclimatic covariates (Pearson et al., 2007, Phillips et al., 2006). Based on this approach, the potential habitat of *V. karroo* beyond the realized niche was identified through matching bioclimatic variables (predictors) to species' presence data (Pearson et al., 2007). Next, the importance of each bioclimatic variable in explaining the spatial distribution of *V. karroo* was determined through iteratively assessing the reduction in the predictive accuracy when the bioclimatic variable of interest is removed from the model (Elith et al., 2011, Phillips et al., 2006). Specifically, the jackknife approach was used to determine the influence of each bioclimatic variable through iteratively excluding the respective bioclimatic variable from the model.

6.2.4.3 Bootstrapping

The bootstrap replicate run method which randomly selects species distribution data without replacement was used for modelling species distribution under different climate scenarios. To do this, 10 experimental runs were executed with a random test percentage of 25 percent of the records for each climate scenario under consideration in MAXENT (Phillips et al., 2006). The selection of a random seed ensures that a separate test/train dataset was available for each of the 10 replicate models (Bean et al., 2012). Due to limited number of species occurrence record (70 occurrence records), data were not exclusively separated into test and training data. To overcome this problem, the bootstrapping approach adopted in this study splits the data several times and the performance of the model is assessed against the randomly chosen test dataset. The approach has been shown to be effective in situations where data is limited and would warrant the use of all occurrence data with a random partitioning implemented within each MAXENT experimental run (Bean et al., 2012, Beane and Rentch, 2015, Beane et al., 2013).

6.2.4.4 Model Evaluation

The area under curve (AUC) from the receiver operating characteristic (ROC) plot was used to assess the performance of the species distribution models. The AUC evaluates the ability of the model to correctly predict the fundamental niche of a given species. Baldwin (2009) provides a model evaluation scheme in which values less than 0.5 indicate that the model is no better than random, values >0.5 to 0.7 indicate a fair model, values 0.7 to 0.9 indicate a good model while values > 0.9 indicate excellent model performance. In this study, the performance of the species distribution models ranged from 0.84-0.94 thereby falling within the good to excellent categories. Based on their performance, the models were deemed ideal for predicting the potential habitat of *V. karroo.*

6.2.4.5 Determination of potential changes in *V. karroo* habitat

The Tenth percentile Training Presence (TPTP) logistic threshold was used to convert the habitat suitability maps into binary maps representing suitable and unsuitable areas. (Hounkpèvi et al., 2016, Fandohan et al., 2015). Based on the binary output, changes in the suitable habitat of *V. karroo* under each climate scenario was determined using conditional statements and Boolean logic in ILWIS GIS (ITC, 2002). Specifically, a habitat was considered stable if there was no change in suitability predicted between the current climate (~1960-1990) and each of the future climate scenarios (2070s). A gain in habitat occurred if, based on the current climate, the habitat was predicted as unsuitable but became suitable under a future climate. In contrast, habitat loss habitat was considered as a change from suitable habitat to an unsuitable habitat between the current and future climates.

6.3 RESULTS

6.3.1 Projected changes in climate

Figure 6.1 illustrates the current rainfall (a), projected rainfall (b) and anticipated rainfall anomalies. It is observed that throughout the country rainfall is projected to decrease with major reductions expected in the eastern and central regions. Specifically rainfall is expected to decrease by an average of between 25 mm and 204 mm.

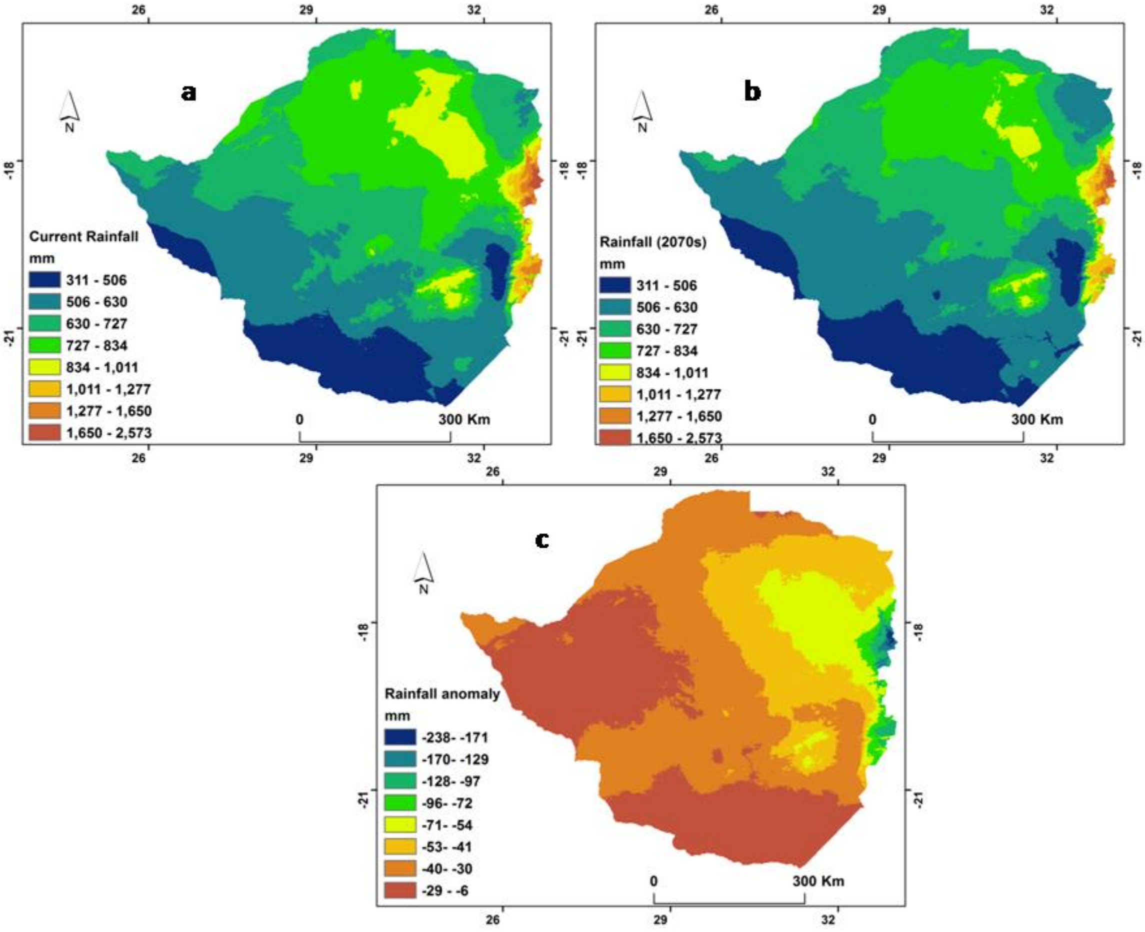

Figure 6.1: Current rainfall (a), average rainfall projected for the 2070s based on the six GCMs (b) and rainfall anomaly (c)

In contrast, temperature is expected to increase by an average of 2.5°C with larger temperature increases projected under RCP8.5 than RCP2.6 across all the GCMs used in this study.

6.3.2 Environmental variables of importance in explaining spatial distribution of *V. karroo*

The key bioclimatic predictors of *V. karroo* habitat suitability under each climate scenario were identified by considering the percentage contribution of each variable to the model. Under the current climatic conditions, BIO9 (Mean Temperature of Driest Quarter), BIO4 (Temperature Seasonality), BIO19 (Precipitation of Coldest Quarter), BIO3 (Isothermality) and BIO14 (Precipitation of driest month) are the most important predictors of *V. karroo* habitat. Combined, these variables explained close to 91% of the habitat suitability model under the current climate with BIO9 being the most important (35.4%). However, under future climates, BIO14 (Precipitation of driest month), BIO4 (Temperature Seasonality) and BIO9 and (Mean Temperature of Driest Quarter) remain key determinants of habitat suitability for *V. karroo*. Overall, BIO9 (35%), BIO14 (19%) and BIO4 (18%) are consistent predictors of habitat suitability of *V. karroo* across almost all GCMs and RCPs considered in this study.

6.3.3 Potential changes to suitable habitat of *V. Karroo*

Table 6-3 and Figure 6.2 illustrate the projected changes in the area suitable for *V. karroo* species under current and future climate scenarios. It can be observed that across virtually all climate models, except for the NC and CN8.5 models, there is a general increase in the area predicted as bioclimatically suitable habitat for *V. karroo*. Furthermore, although there is a general increase in the suitable area for *V. karroo* species under a changing climate, the increase is not uniform across GCMs and RCPs adopted in this study. For instance, the largest increase in suitable area is projected under GS8.5 (57,594 Km^2) and BC 2.6 (52,795 Km^2), respectively, while the smallest increase occurred under CN2.6 (7,633 Km^2). The suitable areas increased in the eastern, western and south eastern regions of the study area. However, decrease in suitable habitat is only observed under CN8.5 (4,229 Km^2), NO2.6 (8,557 Km^2) and NO8.5 (38,807Km^2). Overall, the suitable habitat of *V. Karroo* is projected to increase by an average of 15,696 Km^2 across all the climate models and scenarios considered in this study.

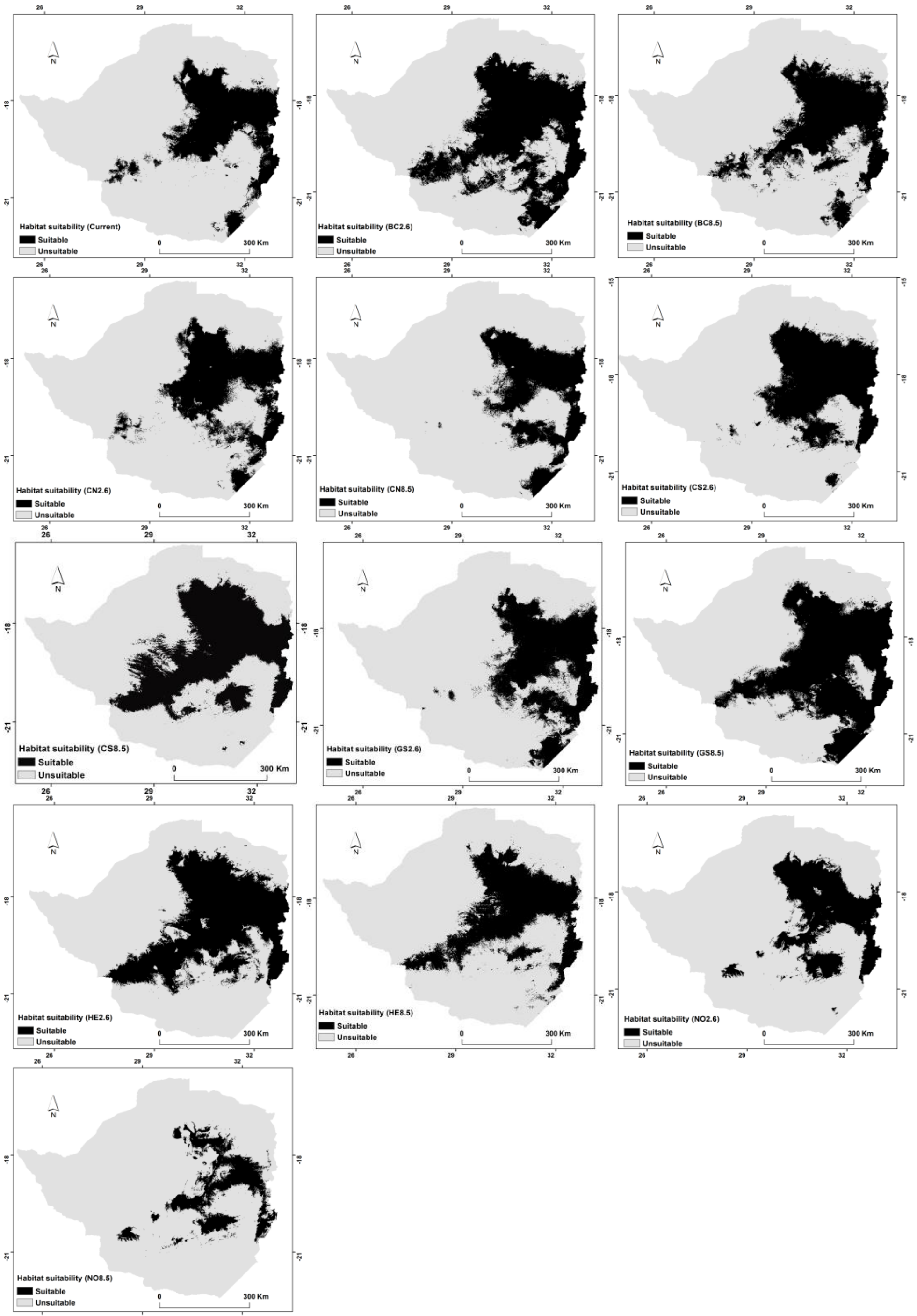

Figure 6.2: Modelled V. karroo habitat suitability under 12 climate scenarios based on the 10 percentile training presence logistic threshold. Suitable and unsuitable refer to areas that are modelled as bioclimatically suitable and unsuitable habitat for the focal species, respectively.

Table 6-3: Changes in the suitable habitat of *V. karroo* projected under twelve (12) climate scenarios based on the 10 percentile training presence logistic threshold. Positive and negative values indicate an increase and a decrease in suitable habitats, respectively.

Scenario	Suitable area (Km^2)	Suitable Area (%)	Change in suitable area (Km^2)	Change in suitable area (%)
Current	83,674	21		-
BC2.6	136,469	35	52,795	63
BC8.5	100,226	26	16,552	20
CS2.6	97,266	25	13,592	16
CS8.5	100,026	26	16,352	20
CN2.6	91,307	23	7,633	9
CN8.5	79,445	20	-4,229	-5
GS2.6	100,062	26	16,388	20
GS8.5	141,268	36	57,594	69
HE2.6	129943,	33	46,269	55
HE8.5	96,445	25	12,771	15
NO2.6	75,117	19	-8,557	-10
NO8.5	44,867	11	-38,807	-46
Average	104,325	25	15,696	19

Figure 6.3 illustrates the gains and losses in suitable habitats of *V. karroo* modelled under each of the twelve climate scenarios. Overall; the percentage gain in suitable habitat of *V. karroo* across virtually all climate scenarios considered in this study is greater than the percentage loss in suitable habitat. Also, it is observed that the gain or loss in the suitable habitat of *V. Karroo* appears dependent on the climate change scenarios used. For instance, the maximum gain in

suitable habitat is projected under the GS8.5 climate scenario while the largest decrease is projected under NO8.5. In addition, there is a general east-west expansion in the distribution of *V. Karroo*. In contrast, most of the projected losses are experienced in the east and central parts of the country in nine of twelve scenarios used in this study.

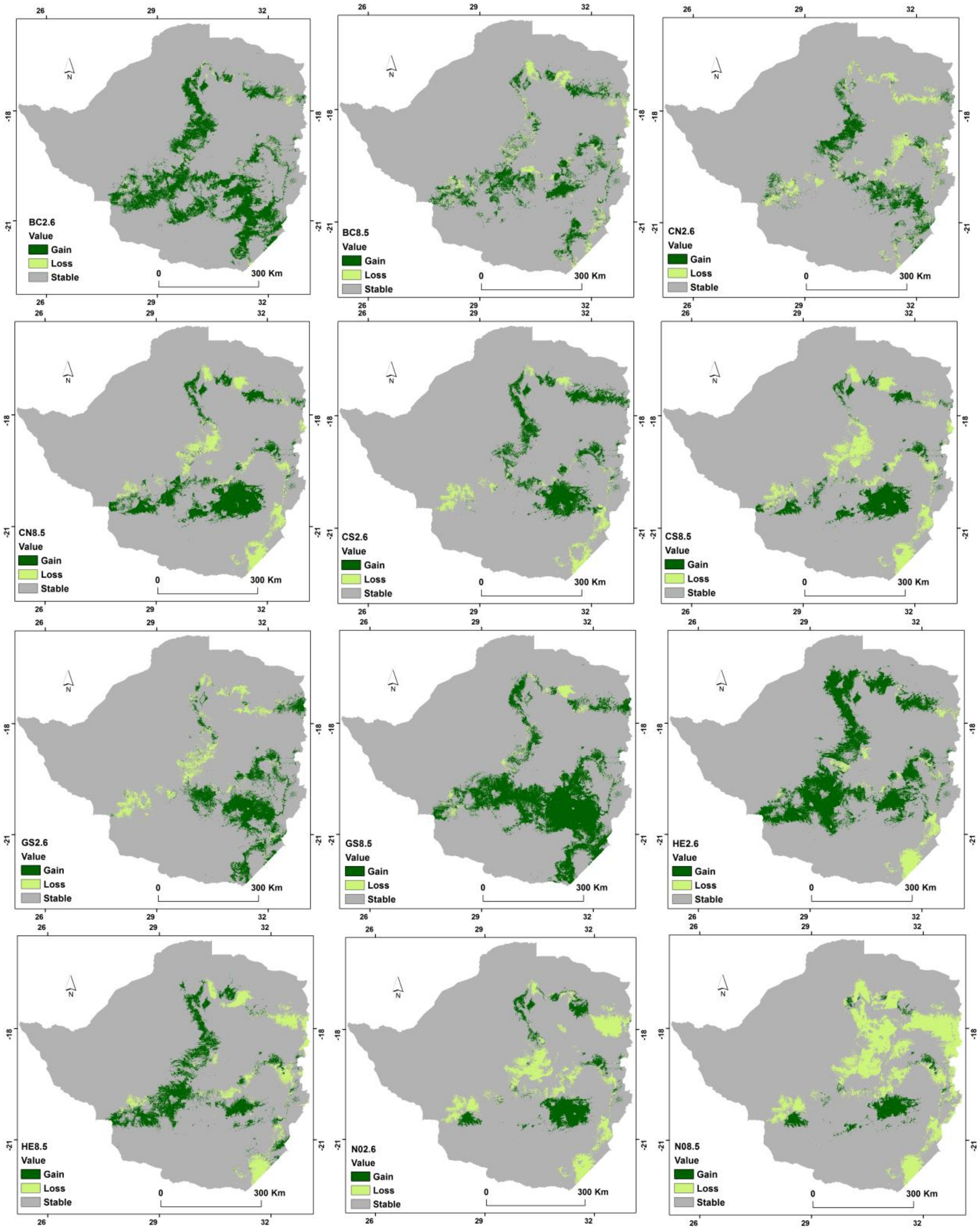

Figure 6.3: Gains, losses and stability in the suitable habitats of V. karroo species projected under different climate scenarios based on the 10 percentile training presence logistic threshold. Gains represent areas that are currently bioclimatically unsuitable for the target species but become suitable under a future climate. In contrast, losses show areas that are bioclimatically suitable under current climate but become unsuitable under a future climate scenario. Stability refers to areas that remain as suitable or unsuitable under a future climate scenario.

6.4 Discussion

6.4.1 Bioclimatic variables of importance

In this study, results indicate that temperature related variables appear more important than precipitation related variables in predicting the spatial distribution of *V. karroo*. For instance, BIO4: Temperature Seasonality and BIO9: Mean Temperature of Driest Quarter are key predictors of *V. karroo* habitat suitability. In contrast, precipitation related variables such as BIO14: Precipitation of driest month are less important in explaining the bioclimatically suitable habitat of the study species. Since *V. karroo* is tolerant to all but extreme frost and droughts, it is therefore not surprising that Mean Temperature of Driest Quarter as well as Temperature seasonality emerged as key determinants of the spatial distribution of the focal species. Given that projections point towards a warmer future climate, results of this study may imply that the habitat of *V. karroo* may expand to mountainous areas that are currently unsuitable due to recurrent frost. In fact, previous studies have shown that cold adapted-plants have been decreasing on mountain summits while warm-adapted species are increasing (Evangelista et al., 2016, Gottfried et al., 2012, Pauli et al., 2012) and this trend is likely to persist in a warmer future.

Results also show that BIO14 (Precipitation of driest month) consistently predicted the bioclimatically suitable habitat of *V. karroo* species across GCMs and RCPs used in this study. Previous studies have highlighted the importance of precipitation as a key factor regulating the physiology and spatial distribution of a several plant taxa (Woodward, 1987) including woody cover in savanna ecosystem (Sankaran et al., 2008). *V. karroo* is a drought resistant woody species that might tolerate all except the most severe droughts. It is therefore intuitive that the distribution of *V. karroo* is determined by moisture availability in the driest quarter. Indeed, results of the species distribution modelling indicated that the bioclimatically suitable habitat of *V. karroo* may likely increase despite the projected decrease in precipitation and rising temperatures. This study joins previous work that has highlighted the importance of precipitation in determining woody species distribution within a changing climate (Shekede et al., 2016, Sankaran et al., 2008).

6.4.2 Potential effects of climate change on the bioclimatically suitable habitat of *V. karroo*

This study tested whether and in what direction the bioclimatically suitable area of *V. karroo* is likely to shift in response to projected changes in climate. Results of this study indicate a general increase in suitable habitat for *V. karroo* species under a drier climate suggesting the likelihood of woody densification in the savanna ecosystem. Although it is unexpected that the suitable habitat for *V.karroo* would increase with decreasing rainfall, these results are confirmed by previous paleo-climatic studies that observed an increase in savanna-dominated landscapes under a drier and warmer climate (Willis et al., 2013). In fact, *V. karroo* is already widespread under current climate showing its ability to survive under a range of climatic conditions (Giannini et al., 2008) including in arid and semi-arid regions. In addition, Lehmann et al., (2011) have demonstrated that African savannas occupy arid-environments that are beyond the lower precipitation limits of savannas elsewhere further providing evidence of the ability of savanna species to survive in water limited environments. Thus, it is deduced that woody species are likely to increase their range and density under a drier and warming climate in Southern African savannas.

Results of this species distribution modelling show a directional expansion of *V. karroo* distribution towards drier areas compared with wetter eastern regions for nine of twelve scenarios used in this study. The observation of general losses in wetter areas (eastern and mountainous parts of the country) coupled with gains in relatively drier areas (central to western parts) differ from previous modelling and observation studies that have observed a consistent upward shift of plant species towards wetter areas such as mountain peaks with changes in climate (see Lenoir and Svenning, 2014 for a review of the studies). The directional shift in the habitat of *V. karroo* towards drier regions could be explained by the fact that the focal species is drought-resistant and has extensive root system (Barnes et al., 1996) which gives it comparative advantage in arid and semi-arid savannas. Moreover, woody species have been shown to adjust their morphological and physiological traits in response to moisture stress (Grossiord, et al., 2017) thereby enabling them to adapt to stressful environments. Insights gained into the potential distribution of *V. karroo karoo* under a changed climate could provide useful knowledge that is critical for savanna ecosystem management in a changing environment.

To date, studies have shown that savannas are undergoing structural changes characterised by an increase in woody cover at the expense of herbaceous layer a global phenomenon known as woody encroachment (Archer et al., 1995). Given that the bioclimatically suitable habitat of *V. karroo* is projected to generally increase across nine of the RCPs based on six GCMs used in this study, it is likely that woody expansion in formerly grass dominated landscapes is likely to persist in future. The increase in woody species in former grass dominated landscapes is often perceived as negative as it reduces the ability of savanna ecosystems to provide goods and services (Lesoli et al., 2013, De Wit et al., 2001). For instance woody encroachment results in loss of biodiversity, reduction in capacity of rangelands to support livestock and wildlife, reduced surface stream flows, increase in fire hazards as well as soil erosion (Kgosikoma et al., 2012, Kgosikoma and Mogotsi, 2013, Lesoli et al., 2013, Moleele, 2002, O'Connor et al., 2014, Wigley et al., 2009). However, positive impacts of woody encroachment such as improved resource stocks (e.g., belowground Carbon and Nitrogen or aboveground NPP), increased animal and plant species diversity have also been reported (see Eldridge et al., 2011). In view of the potential negative effects of woody encroachment on savanna ecosystem and projected increase in the bioclimatically suitable area, monitoring and management efforts could target these woody encroachment “hotspots”. In other words, results from this study could provide a basis for identifying areas for targeted control of encroacher species in savanna ecosystems. In these “hotspots”, multiple strategies for managing woody encroachment such as prescribed burning, mechanical clearing and herbicide application can be implements. However, since the success of woody encroachment has been spatially highly variable (Archer et al, 2017), it is important that rangeland managers use location-specific knowledge of vegetation complexes, climate and soils in order to determine not only the sequence but timing of treatments.

Results indicate that while the bioclimatically suitable range of *V. karroo* species is projected to either contract or expand, overall, the majority of the GCMs and RCPs used this study point towards range expansion of the focal species. Although it would have been informative to provide rates of encroachment, absence of future climate data at a finer scale made it impossible to determine the rates. Several mechanisms may explain the potential range expansion of the target species under a drying climate. *V. karroo* has deep root system which gives it the ability to access water from deeper layers (Barnes et al., 1996) thereby making it drought resistant. A recent study carried out in tropical savanna and forest biomes of Africa and South America has shown that aridity favours Nitrogen fixing plants such *V. karroo* (Pellegrini et al., 2016). Furthermore, since *V. karroo* is capable of fixing Nitrogen, it is able to access resources such as water that are often unavailable to other plants in savannas where nitrogen is limiting. The high water-use efficiency of woody species such as *V. karroo* under elevated CO_2 concentrations is likely to expand the species range to drier sites (Feng et al., 2004, Rogers et al., 2006). Given these positive traits which confer comparative advantage to *V. karroo* over other species, it is likely that the distribution of the target species is likely to track changes in climate.

Results of this study indicate that changes in habitat suitability i.e. either gains or losses in suitable habitat are dependent on the GCM and RCP used in the species distribution modelling. Specifically, under a future changed climate, contractions and expansions in suitable habitat are more heterogeneous across climate models suggesting differential response of *V. karroo* to different magnitude of change in the bioclimatic variables (Trisuart et al., 2011). These results imply that the future woody species distribution modelling is associated with uncertainties. This is confirmed by previous studies that identified the main sources of uncertainty in niche-based SDM as initial dataset conditions (sample size), model classes (e.g. climate model), model parameters (e.g., thresholds used in defining suitability), and boundary conditions e.g., Global Climate Models with different RCPs (for example see Zhang et al., 2015). In this regard, future studies could focus on ensemble species distribution modelling with the aim of focusing on areas of consensus among these climate models.

Unlike most previous studies on the effects of climate change on species distribution, our study has spatially assessed the potential effects of climate change on a key species in southern African savanna ecosystems that tend to thrive in arid to semi-arid and disturbed environmental conditions. Previous studies (Delire et al., 2008, Zelazowski et al., 2011, Dhlamini, 2010) mostly focused on climate change impacts on vegetation at biome level without explicitly focusing on the response of specific species in a spatial domain (Tews and Jeltsch, 2004 , Tietjen et al., 2010). While biome level studies provide important insights into the response of vegetation at a much larger scale, the approach does not account for species-specific response to climate change. Knowledge on species specific range shifts at fine spatial scale is critical for management of woody encroacher species in savanna ecosystems.

Results in this study could provide important insights into the potential effects of climate change on the distribution of *V. karroo* species. However, since climate is changing simultaneously, and interacting, with other global environmental changes such land use change; the ultimate extent of *V. karroo* could be determined by an interaction of several factors. For instance while precipitation is a key determinant of the distribution of woody cover, land use can be critically important to the extent of even counteracting the effects of climate change (Aleman et al., 2017). Indeed, under-or over-estimation of actual species distributions can result from omission of land use variables in species distribution models thereby hindering the understanding of climate change impacts on the habitat of woody species in savannas (Ay et al., 2017). Similarly, nitrogen and carbon dioxide are projected to increase in future and may also influence the future spatial distribution of woody species (Buitenwerf et al., 2012, Kraaij and Ward, 2006, Sankaran et al., 2008, Shanahan et al., 2016). The incorporation of these variables in species distribution models could therefore increase the understanding of the structure of ecosystems such as savannas within the context of global environmental changes.

6.5 Conclusion

The aim of this study was to test whether and how climate change is likely to affect the spatial distribution *V. karroo*, a key woody species in a water-limited southern African savanna based on six Global Circulation Models representing climate of the 2070s and a set of geo-referenced species occurrence data. Based on the results of this study it is concluded that bioclimatically suitable habitat of *V. karroo* is likely to significantly increase under a changing climate in southern African savannas. In addition, the areal expansion of *V. karroo* habitat is directional and tracks changes in the direction of the projected changes in rainfall. Besides the directional expansion of *V. karroo* habitat expansion, the magnitude of the response of *V. karroo* to climate change is dependent on the assumed Global Circulation Model as well as Representative Concentration Pathway. Results of this study could be useful in targeting management of woody encroachment under a changing climate as it identified areas at risk of *V. karroo* encroachment, stable areas and areas likely become unsuitable for the focal species. These results imply that the adoption of species based modelling could provide important insights into the potential effects of climate change on the structure of savanna ecosystems and is key for management of savannas in the context of global environmental changes.

Chapter 7 Synthesis

Tree-grass interactions under a changing environment

7.1 Introduction

The distinguishing feature of savanna ecosystems is the co-dominance of woody and herbaceous species in the same landscape (Scholes and Archer, 1997). The co-dominance of these two life forms makes savanna ecosystems ecologically and socio-economically important as they support millions of livelihoods through wildlife and livestock production (Sankaran et al., 2008). However, the co-dominance of woody and herbaceous species is changing as a result of, among other factors, changes in rainfall patterns and nutrient fluxes in the ecosystems resulting from global environmental changes (Kgosikoma and Mogotsi, 2013, O'Connor et al., 2014, Roques et al., 2001). Changes in this co-dominance have mainly been observed through increasing levels of woody cover in savannas (Archer et al., 2017, Buitenwerf et al., 2012, Eldridge et al., 2011). Although, the increase in woody cover, herein referred to as woody encroachment is now a widespread global phenomenon (Wigley *et al*., 2009), the mechanisms that drive this ecological process have remained elusive (Ward 2005, Wigley *et al*., 2010, Devine *et al*., 2017). Thus, new and innovative approaches need to be developed or adopted in order to aid understanding of woody encroachment as well as the mechanisms behind it.

In this study, the main objective was to understand whether and in what direction changes in key resources i.e., rainfall and nitrogen alters tree-grass interactions in semi-arid southern African savannas. The specific objectives of this thesis were to: (1) develop an approach that can be used to successfully detect woody encroachment based on remotely sensed data as a preamble to understanding effects of rainfall on woody patch dynamics in savannas, (2) test the extent to which rainfall variability explains woody encroachment, (3) determine how and whether rainfall suppression alone and its interaction with nutrient addition significantly influence woody sapling growth, and, (4) investigate the potential effects of climate change on the potential distribution of characteristic woody species in southern African savannas based on Global Climate Change projections.

7.2 Woody species establishment and dynamics under a changing environment

7.2.1 The intensity-dominant scale framework offers an objective method of characterising subtle changes in woody cover

Understanding mechanisms underlying subtle changes in woody cover especially those associated with woody encroachment in savanna ecosystems require objective methods that can characterise this ecological process. While significant progress has been made in characterising woody encroachment (Britz and Ward, 2007, Hudak and Wessman, 2001, Moleele, 2002), protocols and methods that have been developed so far have often failed to determine the window size, that is, the scale at which woody encroachment occurs. This situation is untenable since ecological processes such as woody encroachment are intrinsically scale dependent (Wiens, 1989; Wiegand et al., 2006). In addition, previous studies have not adopted any analytical framework that concurrently incorporate vegetation cover dynamics and scale at which linear dimension of wood patches are expressed (but see Murwira and Skidmore, 2005, Pittiglio et al., 2011). This thesis applied the intensity-dominant scale approach anchored by wavelet theory and succeeded in objectively characterising woody encroachment at multiple Zimbabwean savanna sites. This approach was adopted as a first step towards understanding the magnitude and direction of change as well as to gain insights into the possible mechanisms driving woody encroachment.

The study demonstrated that wavelet transform implemented within the dominant scale framework provides a promising, objective and repeatable approach for characterising subtle woody patch expansion, contraction and/or densification. The findings in Chapter 2 indicate that when coupled with integration of remotely sensed data from multiple sensors, the intensity-dominant framework implemented using wavelet transform is able to simultaneously capture the spatial extent of woody encroachment and intrinsic characteristics of woody patch dynamics. This approach is an improvement from previous studies that have attempted to characterise woody encroachment in savannas using traditional approaches such as simple image classification and thresholding (Hudak and Wessman, 2001, Moleele, 2002, Wiegand et al., 2006). In fact, this new approach affords researchers and environmental managers an opportunity to overcome inaccuracies and inconsistencies that are often associated with quantifying woody encroachment in savanna ecosystem (Odindi et al., 2016, Mansour et al., 2013). Indeed, the main limitation of previous approaches is their failure to capture the morphology of savanna ecosystems characterised by co-dominance of woody and grass cover (Pittiglio *et al.,* 2011). In other ecosystems these two life forms normally exclude each other. This complex morphological structure could partly explain the high inaccuracies in savanna that are inherent in landcover maps (Pittiglio et al., 2011).

This thesis has clearly shown that the intensity-dominant scale framework enables the integration of multi-resolution and multiple sensor data i.e., aerial photographs and satellite images with different radiometric and spatial resolution to quantify woody encroachment. This builds on previous work in which only one source of data was exploited. The ability to integrate various remotely sensed datasets makes it possible to utilise archival data of aerial photographs. This makes it possible to extend the temporal scale at which woody encroachment is analysed since the first satellite images became available in the early 1970s whereas aerial photography was developed much earlier. This capability opens avenues for testing ecological hypotheses related to woody encroachment, a phenomenon that may express itself in the landscape over decadal or larger time scales. The integration of remotely sensed data with different timescales and radiometric resolution based on the intensity-dominant scale framework hinges on the fact that intensity is a normalised measure of contrast in dominant landscape features such as grass or woody patches. In addition, the intensity-dominant approach can detect woody encroachment as long as the spatial scale of the process is greater than the pixel size.

A key insight into woody encroachment gained by using the wavelet transform within the intensity-dominant scale approach is that although the dominant scale (i.e., the average patch size) can remain the same while the intensity changes. For example, at Chivero Game Reserve, it was observed that the dominant scale did not change between 1985 and 1996 yet intensity increased during the same time (Chapters 2 and 3). Such a result implies that the extent of woody patches might remain the same but the density of woody species in the woody patches may increase. Since previous studies (Archer et al., 1994, Britz and Ward, 2007, Hudak and Wessman, 2001, Marston et al., 2017, Moleele, 2002, Wang et al., 2018, Wigley et al., 2009) overly relied on traditional methods of image processing to quantify woody encroachment, they could have underestimated dynamics of woody cover in savanna ecosystems. Thus future studies need to quantitatively assess the performance of these traditional methods of estimating woody encroachment against the approach used in this study.

7.2.2 Decadal changes in precipitation drive woody patch dynamics in savannas

Rainfall has long been recognised as a key determinant of savanna ecosystem structure and functioning (Walter, 1971). In this regard, several studies have attempted to quantitatively relate changes in woody cover to changes in rainfall (Good and Caylor, 2011, Devine et al., 2017, Sankaran et al., 2005, Sankaran et al., 2008). For example, using field data from many sites distributed across the African continent, Sankaran et al., (2008) observed a consistent positive relationship between mean annual rainfall and woody cover. This finding suggests that savannas are water-limited ecosystems. The contribution of this thesis is that the universality of this relationship depends on how accurately woody cover is estimated in the first place. For instance, attempts to estimate the extent and dynamics of woody encroachment have mainly relied on traditional approaches such as digitising of aerial photographs (Roques et al., 2001, Wigley et al., 2009), textural analysis (Hudak and Wessman, 2001) and classification of multi-temporal satellite images (Skowno et al., 2017, Teka et al., 2018). These methods are subjective and susceptible to human error (Mansour et al., 2013). To overcome this limitation, wavelet transform was first applied within the intensity-dominant scale framework to objectively characterise woody encroachment before relating the observed woody cover changes to decadal mean annual rainfall.

This approach created an opportunity to evaluate the importance of rainfall as a driver of woody cover change. Specifically, results of this thesis (Chapter 3) demonstrate the existence of a signficant asymmetrical U-shaped relationship between changes in decadal mean annual rainfall and dominant scale. In line with previous work (Sankaran et al., 2008; Buitenwerf et al., 2012), this finding provides the first quantitative evidence on how decadal changes in mean annual rainfall trigger changes in the dominant scale of woody and grassy cover in a savanna landscape. In southern Africa, this study is interesting because it ties well with previous work from Climate Science studies that indicate that the region experiences drought at a seven to ten year cycles (Masih et al., 2014, Tyson, 1991(Tyson, 1991). This work together with existing knowledge could provide an opportunity for ecologists to use the ten year domain as the temporal window in which they can characterise woody cover dynamics if they are using rainfall.

Furthermore, the asymmetrical U-shaped relationship between decadal changes in rainfall and changes in woody patch size suggest typical high sensitivity of woody patches to rainfall variability in savannas. This can be deduced from the fact that that changes in woody patch size as a function of rainfall variability are more rapid during low rainfall periods (drought) compared to how they respond during wet periods (see Figure 3.5 in Chapter 3). This result implies greater response of woody species to water stress compared to moisture surplus. Thus, this finding might be useful in understanding the potential effects of increased frequency and severity of droughts that are anticipated under a future climate (IPCC, 2014). For example, rangeland managers may take advantage of extreme low rainfall (droughts), the period during which woody plants are hypothesised to be at their weakest, and use fire to control recruitment and growth (Roques et al.

2001, Kgosikoma and Mogotsi 2013) as a strategy to manage woody encroachment. In other words, increase in woody encroachment experienced during years with rainfall pulses could easily be offset if management actions coincide with the temporal scale at which droughts have significant negative effects on woody patches (Fensham *et al*. 2009). While insights into how rainfall variability at decadal scales affect savanna structure from multiple sites located along a rainfall gradient have been gained in this study, there is need to test the applicability of this framework to other sites in order to evaluate whether the proposed conceptual framework can be extended to other savanna sites. Also, the approach adopted in this study allows for the incorporation of other drivers of woody cover change such as overgrazing and CO_2 fertilisation, to gain a better understanding of the relative importance of factors driving woody cover dynamics in savanna ecosystems. Thus, the thesis provides opportunities for other researchers to accurately characterise woody cover dynamics while accounting for the observed change.

7.2.3 Effects of moisture availability on woody sapling recruitment

Several climate change models indicate that in southern Africa rainfall is likely to change by different magnitude and in different directions in future. For instance, summer rainfall projected to decrease by between 4 and 30% while temperature is expected to increase by 3 °C by the end of the 21st century (IPCCC, 2007, 2014). Thus, an increase in temperature accompanied by a reduction in rainfall point towards a future climate characterised by moisture stress. However, it is not clear how savanna vegetation will respond to the projected decrease in precipitation.

Results showed that an experimentally imposed 15% reduction in rainfall under field conditions at a protected Zimbabwean savanna site affects the growth (i.e., sapling diameter and height) of *V. Karroo* in the early stages of growth (Chapter 4).Thereafter, the effects of rainfall supression on growth became statistically insignificant. This result is inconsistent with findings by Barbosa et al., (2014) who did not detect significant effects of water availability in the early stages of seedling development of eight common species from different functional groups at a semi-arid South African savanna site. This result implies that the early stages of woody species establishment are more sensitive to changes in moisture availability than the later stages of growth, a result that is in accord with previous work (Sankaran et al., 2008, Scholes and Archer, 1997, Van Der Waal et al., 2009). Successful woody seedlings recruitment is therefore critical as it determines whether the species will increase in abundance and thereby influence savanna structure and functioning for example through release of more litter and nutrient cycling (Cramer et al., 2010, February et al., 2013).

The experimental work also revealed that woody plants growing under rainfall suppression allocated more biomass towards diameter growth than height increment (Chapter 4) across the growing season. The results imply that in response to moisture stress, *V. karroo* saplings tend to prioritise diameter growth and by inference root foraging (Archibald and Bond, 2003, Poorter and Nagel, 2000). Since a drying trend is projected for southern African savanna (IPCC, 2007, IPCC, 2014), the persistence of savannas will be dependent on the ability of woody species to adapt to the changes in rainfall patterns (Barbosa et al., 2014).

The lack of overall significant effects of rainfall suppression over the duration of the experiment suggests that the projected 15% decrease in total precipitation over southern Africa may still be within the optimal range for the growth of *V. karroo* saplings (Chapter 4). This result is supported by previous studies that observed similar growth rates between plants exposed to moderate moisture stress and those growing under normal rainfall conditions (Padilla et al., 2009, Poorter et al., 2012). Similarly, in a study to test the effect of water supplementation on germination and seedling establishment of eight dominant savanna species, Barbosa et al., (2014) failed to detect significant effects of increased water availability.

The failure to detect overall significant effects of rainfall suppression at a local scale in which savanna trees interact with grasses are in line with findings of the ecological niche modelling that suggest the bioclimatically suitable habitat of *V. karroo* habitat may expand in future (Chapter 6). In a recent study, Pellegrini et al., (2016) showed that aridity more than fire confers comparative advantage to Nitrogen-fixers such as *V. karroo* thereby enabling the species to survive under a range of environments. It has also been reported that it is only when plants are subjected to severe moisture stress that they may increase in allocation to roots at the expense of stems (Poorter et al., 2012). In this regard, future work need to experimentally test the thresholds beyond which water availability causes significant effects on woody species growth. This information could be critical for understanding the levels of precipitation decreases that are likely to change the balance of tree-grass ratios typical of savannas, thus potentially changing the range of services such as carbon sequestration offered by these unique ecosystems..

7.2.4 Effects of nutrient enrichment on woody sapling recruitment

The increase in nitrogen deposition being experienced in terrestrial ecosystems across the globe is affecting the structure and function of ecosystems (Bobbink et al., 2010, Phoenix et al., 2006, Valliere et al., 2017, WallisDeVries and Bobbink, 2017, Van Der Wal et al., 2003). Studies have yielded mixed results regarding effects of N enrichment on the recruitment of woody species in savannas. For instance positive effects of N deposition have been reported in temperate grasslands (Kellman, 1989, Köchy and Wilson, 2001) while data from several field experiments in savanna sites have shown negative effects of N fertilization on woody species through increased suppressive effects of grasses under high nutrient levels (Cohn et al., 1988, Cramer et al., 2010, Riginos, 2009, van der Waal et al., 2009). In other studies no significant effects of N fertilisation were detected on woody species recruitment (Barbosa et al., 2014a, Sankaran et al., 2008, Schlesinger et al., 1996). These contrasting findings suggest that the effects of N on terrestrial ecosystems are idiosyncratic and still poorly understood.

In this study (Chapter 5), a field experiment was performed to test the effects of N supplementation on the growth of *V. karroo* saplings in semi-arid savanna of southern Africa in the presence and absence of grass competition. It was predicted that sapling growth would increase with nutrient availability as energy that would otherwise be allocated to Nitrogen fixation would be assigned to growth. Results from the four-year experiment showed that N fertilisation alone did not significantly influence the growth of *V. karroo,* though saplings exposed to N addition had shorter but had larger stem diameter compared to the control. While contradicting the expected, the results are in line with previous studies that either observed a reduction in woody species growth as a result of N addition (Schuster and Dukes, 2017) or found no effects of N addition on the growth of woody seedlings in semi-arid savannas (Mopipi et al., 2009, Van Der Waal et al., 2009, Xia and Wan, 2008). Indeed, the growth of leguminous woody species such as the genus *Vachellia* can be insensitive to N addition compared to the addition of other mineral nutrients such as phosphorous as demonstrated previously (van Auken et al., 1985). The inference that can be drawn from the results in Chapter 5 interpreted in the context of other relevant work is that responses of woody species to N addition particularly N-fixers will be contingent on the levels of other resources such as phosphorous and water since these resources co-limit woody species recruitment in savanna ecosystems. Furthermore, although it was not the main focus of this thesis to account for the multiple pathways through which N is accessed by plants, the failure to detect significant effects of N on *V.karroo* sapling growth could be partly attributed to our failure to consider the several pathways through which N is acquired by plants. In the experiment, N was place applied as Ammonium nitrate to gain insights into how nitrogen fertilisation would influence tree grass interactions. Thus, future studies need to set up experiments that incorporate the multiple pathways through which N is absorbed by plants in order to fully mimic nitrogen deposition.

7.2.5 Combined effects of rainfall suppression and N addition on woody sapling recruitment

Climate change is projected to influence not only distribution but also amount of rainfall during the rainfall season across the globe. For southern Africa rainfall projections point towards a drier climate coupled with an increase in ambient temperatures. At the same time, N deposition to terrestrial ecosystems is increasing across southern Africa due to increased vehicular emissions and industrialisation. However, the combined effect of changes in these two key resources limiting plant growth in semi-arid savannas of southern Africa is poorly understood. Specifically, it is not clear how decrease in precipitation and increase in N deposition will likely affect tree-grass interactions in savanna ecosystems.

Results of this study (Chapter 5) indicated that significant effects of N addition were only detected when N interacted with rainfall suppression suggesting that moisture availability mediates the effect of N addition. However, the interaction effects between rainfall suppression and N addition was only observed in the second season and not thereafter. This suggests that the positive effect of N addition may be cancelled out by rainfall suppression over time. This is perhaps the first time that the transient effects of N and rainfall suppression on N-fixer woody species have been reported in semi-arid savannas. In fact, N fertilization under reduced rainfall could increase plant tolerance to soil moisture stress (Kinugasa et al., 2012) through, for example, increasing below ground biomass (Van den Driessche, 1992). Studies elsewhere have shown that N-fixing plants are capable of sustaining high foliar N concentrations leading to efficient water use (Adams et al., 2016). Thus the results in Chapter 5 are confirmed by previous research that observed significant interactive effects of nutrient addition and water manipulation on woody seedling growth suggesting mediating effect of rainfall reduction on the growth of *V. karroo* saplings (Adams et al., 2016).

7.2.6 Effect of grass competition on woody sapling recruitment

In savanna ecosystems where trees and grasses achieve dynamically stable coexistence, grass competition is considered a key mechanism limiting the transition of woody seedlings into adult trees thus leading to co-dominance(Chesson, 2000). Grasses are known to be more efficient in utilising resources in the upper layer thus pre-emptying their use by woody seedlings (Melina et al., 2015, Riginos, 2009, Vadigi and Ward, 2013). In addition, grasses directly provide fuel load for fires which prevents tree seedlings and juveniles from escaping the flame zone thereby limiting tree recruitment. However, the widespread increase in woody species being observed in savannas challenges this notion. Using *V. karroo* as a test species, this study investigated whether grass competition significantly reduced the growth of the woody species when exposed to nutrient enrichment and moisture stress.

Results from this study, indicated that neither grass competition alone (Chapter 4) nor its interaction with either N fertilisation (Chapter 5) or rainfall suppression (Chapter 4) had significant effects on the growth of *V. karroo* saplings. These results are inconsistent with previous studies that reported suppressive effects of grass competition on woody species across all growth stages (Cramer et al., 2007, Knoop and Walker, 1985, Vadigi and Ward, 2013, Van Der Waal et al., 2009). However, lack of suppressive effects of grasses on woody species especially N-fixers has been previously documented (O'Connor, 1995). Evidence from recent ecological studies is pointing towards increasing role of facilitation over competition under conditions of abiotic stress (Callaway, 2007, Dohn et al., 2013, He et al., 2013, Maestre et al., 2009); with the largest facilitative effects reported at intermediate stress levels (Holmgren and Scheffer, 2010).

Facilitation has been observed in ecosystems receiving relatively high amounts of rainfall of up to 1800 mm suggesting that facilitation maybe widespread than previously thought (Mazía et al., 2016). The 15% experimentally reduced rainfall could have resulted in marginal stress. Thus it is postulated that the marginal stress could have enhanced facilitation between grasses and woody saplings for resources such as Nitrogen since N-fixers have been shown to transfer fixed N to non-legume species (Sierra and Nygren, 2006, Zhang et al., 2016). In agreement with previous studies, results of this study suggests that grass swards ameliorate soil and thermal stress through providing shade thereby facilitating the growth of woody saplings (Joubert, 2014). Thus the results of this work point towards the potential role of facilitation in shaping plant communities even under marginally stressful conditions.

7.2.7 Climate change and woody species distribution in southern African savannas

The projected decreases in rainfall combined with increases in temperature in southern Africa may have significant impacts on the savanna ecosystems, yet it is currently not clear how and whether the anticipated decrease in rainfall will alter the structure of the savanna ecosystem. Results of this thesis (Chapter 6) have shown that, despite the projected decrease in rainfall across different Global Climate Models and Representative Concentration pathways considered in this study, the bioclimatically suitable habitat of *Vachellia karroo* species is likely to increase in future. While this result seem counterintuitive, previous studies observed that savanna landscapes expanded under a drier and warmer climate based on paleo-climatic data (Willis et al., 2013). Similarly, Lehmann et al., (2011) demonstrated that African savannas are located in regions with relatively limited rainfall as long as fire was absent thereby showing the ability of savanna species to survive in water limited environments. The fact that *V. karroo* is already widespread under current climate showing its ability to survive under a range of climatic conditions (Giannini et al., 2008) including in arid and semi-arid regions. Thus, it is deduced that woody species are likely to increase their range and density under a drier and warming climate in Southern African savannas.

Savannas are undergoing structural changes characterised by an increase in woody cover at the expense of herbaceous layer (Archer et al., 1995). Given that the bioclimatically suitable habitat of *V. karroo* is projected to generally increase, it is likely that woody expansion in savanna landscapes is likely to persist in future. Although the increase in woody species in savannas has both positive (e.g., forage for browsers, household fuel-wood provision, increased carbon sequestration) and negative impacts, it is often perceived as negative. (Lesoli et al., 2013, De Wit et al., 2001). For instance woody encroachment results in biodiversity loss, reduction in capacity of rangelands to support livestock and wildlife, reduced surface stream flows, increase in fire hazards as well as soil erosion (Kgosikoma et al., 2012, Kgosikoma and Mogotsi, 2013, Lesoli et al., 2013, Moleele, 2002, O'Connor et al., 2014, Wigley et al., 2009). Given the potential negative effects of woody encroachment on savanna ecosystem and projected increase in the bioclimatically suitable area of *V. karroo*, monitoring and management efforts could target these areas.

Overall, the thesis has improved our understanding of the effects of key resources on woody species recruitment savanna ecosystem by first developing a framework that detects the scale at which woody encroachment is occurring through integrating multi-temporal satellite imagery and aerial photograph. The ability to detect the spatial scale at which woody encroachment occurs in the landscape improves on previous attempts that failed to capture the scale-dependency of bush encroachment. Moreover, the opportunity to integrate aerial photographs and satellite images provides an avenue for ecologists to test hypotheses on woody encroachment over longer temporal scales than what was previously (Chapter 2). Most importantly, the intensity-dominant framework developed in this thesis enables scientists to test the effect of key resources on woody patch dynamics across savanna landscapes (Chapter 3). Through our experimental work, we were able to tease out the effect of N addition and rainfall suppression on woody species recruitment in a savanna landscape at a neighbourhood scale i,e., plant to plant interactions (Chapter 4 and 5), Results from the study indicate that *V.karroo* species is likely to expand its range and persist in future as indicated lack of significant effects of manipulated resources as well as grass competition, an observation that is in line with those from habitat modelling (Chapter 6). Thus management efforts should be targeted in areas projected to experience increased rates of encroachment.

7.3 Implications for savanna conservation and management

This study has generated important insights into the growth of a dominant woody species in a semi-arid savanna under a changing environment. First, the results from this thesis have shown that using wavelets within the dominant-scale framework, one can simultaneously capture woody densification as well as its expansion. This capability provides rangeland managers with an opportunity to effectively monitor woody cover dynamics in savannas and in turn evaluate the success of management efforts.

Another important result from this study is that savannas are more sensitive to moisture stress than moisture surplus. The understanding of how moisture variability especially influences patterns of tree recruitment and woody patch dynamics in savannas could be critical for managing savannas. Field observations have shown that extreme drought events often coincide with massive tree mortality (Fensham and Fairfax, 2005, Fensham and Fairfax, 2007, Fensham et al., 2003.) and higher herbivory pressure (Holmgren and Scheffer, 2001a). It is therefore likely that during these extremely low rainfall years, trees could be more vulnerable due restricted seed germination, plant growth as well as intense competition for limited water (Roques et al., 2001a). This may lead to natural mass mortality and thus rangeland management strategies such as use of fire could be successful under extreme dry conditions. In this regard, interventions on managing woody encroachment in rangelands could be adjusted to coincide with intense droughts for optimum results. A recent study has shown that using prescribed fire during drought years may significantly reduce rates and extent of woody encroachment in savannas (Twidwell et al., 2016).

Results from experimental work have also shown that rainfall reduction may significantly affect *V. karroo* a key encroacher growth in the early stages of development but not afterwards. This result suggest that once saplings pass a certain critical establishment phase, the effect of rainfall reduction may be counteracted by increased availability of other resources such as nitrogen resulting in compensatory growth. To this end, it is deduced that woody encroacher species will persist under a drying climate. These results are also confirmed by insights gained from species distribution modelling of *V. karroo* species under a future climate which indicated an expansion in the suitable habitat of the focal species despite projections of a drying climate (Chapter 6). Put together, these results point towards the need for incorporating climate change in the management of woody encroachment in savannas.

7.4 Future research

While important insights have been gained from this thesis, there are still a number of areas that require further research. First, in this study we manipulated two key resources i.e., soil moisture availability and Nitrogen in the presence and absence of grass competition. While these two resources are the key determinants of woody species growth in savannas, mediating factors such as fire and CO2 have also been identified as important in shaping the structure of vegetation in savannas. Thus, future research need to experimentally manipulate multiple and interacting resources such as Nitrogen, rainfall, herbivory and CO2, at longer time scales e.g., several decades. Moreover, future studies need to test the effects of changes in resource availability (eg., nitrogen and soil moisture) and disturbances (e,g., herbivory and fire) on tree species recruitment since plant species from different functional groups are expected to differentially respond to these changes. For N manipulation, studies need to incorporate the various pathways through which N is accessed by plants in order to gain insights into how plants will respond to nutrient fluxes in future. This is especially important considering that these key resources are expected to change in the coming decades.

In this study, field multi-factorial experiments in which soil moisture and soil nutrients were manipulated in the presence and absence of grass competition over a four-year period. While results of this study have provided empirical evidence of how woody species, specifically N-fixers might respond to key resources as a result of global environmental changes, the study relied mostly on above ground growth attributes. Thus future studies need to determine effects of changes in key resources on both below-ground and above ground biomass. In this regard, important insights into changes in resource allocation patterns might be gained from such an approach.

Although savannas occur along a wide rainfall gradient stretching from arid savannas, through semi-arid savannas to humid savannas our experimental study was performed at one savanna site receiving 630 mm of rainfall due to limited financial resources,. While important insights on the effects of rainfall and nitrogen on *V. karroo* growth were gained from this study, more insights could have been generated if the study was performed along a rainfall gradient. Thus, it would be interesting for future studies to perform similar experiments along a wider rainfall gradient that include temperate savannas, Asian savannas, American savannas and manipulating similar resources in order to understand the fate of savannas in the context of climate change. Despite the difference in the direction and magnitude of change in climate along the savanna rainfall gradient, the intensity-dominant scale approach used here still allows multi-site comparisons.

Future studies are likely to be more informative if they can manipulate rainfall regimes using projected change in rainfall but outside of the natural variability of rainfall. This approach may, perhaps, offer an opportunity to get improved understanding on the effects of changes in rainfall regimes on savanna ecosystem structure and functioning. In other words, if rainfall manipulation experiments are performed within the rainfall variability of the respective savanna sites, it may confound the effects of rainfall on tree-grass interactions in savannas. Nonetheless, it will be interesting to compare results of such future studies with current study in which experimental plants were subjected to projected moisture rainfall while the control was grown under natural rainfall.

Another important finding from this study is that historical aerial photographs and optical remote sensing images when analysed using wavelet transforms provide an objective method of simultaneously quantifying woody cover and linear dimensions of woody encroachment. This overcomes the shortcomings of previous traditional methods that are often inaccurate, subjective and time-consuming. With the increase in ready availability of satellite imagery such as Synthetic Aperture Radar (SAR) and high resolution imagery such as Sentinel, future studies could test whether the integration of both optical and SAR data significantly improves characterisation of woody species encroachment in savanna ecosystems.

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