ENCROACHMENT DYNAMICS OF *Acacia drepanolobium* IN MASWA GAME RESERVE

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A Dissertation Submitted in Partial Fulfilment of the Requirements for the Degree of Master's in Life Sciences of the Nelson Mandela African Institution of Science and Technology

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ABSTRACT

Habitat degradation, caused in particular by woody plant encroachment, has been a common phenomenon in savanna ecosystems. With increasing woody plant cover in open savanna grassland, structural changes and their associated impact need to be assessed and quantified. We analyzed the extent of woody plant encroachment via remote sensing and assessed encroached sites and open grassland of Maswa Game Reserve on the ground to identify and examine encroaching woody plant species and their associated impacts on herbaceous plant and herbivore species. We found that woody plant cover increased by 0.5% to 2.6% per annum. *Acacia drepanolobium* dominated the woody encroaching species, and the number of stems in heavily encroached sites was seven times and three times higher than in open grassland and at medium encroached sites, respectively. Our results show that woody plant encroachment reduces grazers and mixed feeder species occurrence. Furthermore, the number of herbaceous species slightly increased with increase of woody plant encroachment, while herbaceous cover was negatively correlated with increase of woody plant cover. Fire significantly reduced germination success of *A. drepanolobium*. Intermediate simulated rainfall was more beneficial to seedling emergence success than infrequent simulated rainfall, while seedling shoots growth was significantly higher in frequent and intermediate simulated rainfall treatments than under infrequent simulated rainfall. Hence, our study suggests that the recent bush encroachment phenomena might have been stipulated by suppression of bush fires and frequent low rainfall. This understanding will contribute in management of vegetation specifically woody plants in savanna ecosystems that are important wildlife habitats.

DECLARATION

I, Houssein Samwel Kimaro do hereby declare to the senate of Nelson Mandela African Institution of Science and Technology that this dissertation is my own original work and that it has neither been submitted nor being concurrently submitted for the degree award in any other institution.

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CERTIFICATION

The undersigned certify that they have read and hereby recommend for examination of a dissertation entitled "Encroachment Dynamics of *Acacia drepanolobium* in Maswa Game Reserve" and recommended for examination in fulfillment of the requirements for the degree of Master's in Life Sciences of the Nelson Mandela African Institution of Science and Technology (NM-AIST).

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In the Name of Allah, the Most Merciful, the Most Compassionate all praise be to Allah, the Lord of the worlds; and prayers and peace be upon Mohamed His servant and messenger. First and foremost, I must acknowledge my limitless thanks to Allah, the Ever-Magnificent, the Ever-Thankful, for His help and bless. I am totally sure that this work would have never become truth, without His guidance. I owe a deep debt of gratitude to NM-AIST for giving us an opportunity to complete this work. I am grateful to all people, who worked hard with me from the beginning till the completion of the research project particularly my supervisors Prof. Anna C. Treydte and Dr. Linus Munishi, who have been always generous during all phases of the research, and I highly appreciate comments and the efforts expended by colleagues and Staff of NM-AIST. I also would like to express my wholehearted thanks to my family for their generous support they provided to me throughout my entire life and particularly through the process of pursuing the master degree. Because of their unconditional love and prayers, I have the chance to complete this thesis.

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DEDICATION

This dissertation is dedicated to the citizens of Tanzania, specifically the Tanzania Wildlife Management Authority (TAWA). The context of the research and its findings can be used as basis to make informed decision for proper vegetation management, monitoring and further research in Maswa Game Reserve.

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LIST OF ABBREVIATIONS AND SYMBOLS

≥	-	Equal or greater than
≤	-	Equal or less than
<	-	Less than
ANOVA	-	Analysis of Variance
FCF	-	Friedkin Conservation Fund
GPS	-	Global Position System
IPCC	-	Intergovernmental Panel on Climate Change
MGR	-	Maswa Game Reserve
NCA	-	Ngorongoro Conservation Area
NDVI	-	Normalized Difference Vegetation Index
NM-AIST	-	The Nelson Mandela African Institution of Science and Technology
PAST	-	PAleontological Statistics
SENAPA	-	Serengeti National Park
TANAPA	-	Tanzania National Park Authority
TAWA	-	Tanzania Wildlife Management Authority
TAWIRI	-	Tanzania Wildlife Research Institute
URT	-	United Republic of Tanzania
WPE	-	Woody Plant Encroachment

CHAPTER ONE

INTRODUCTION

1.1 Background

Habitat degradation, caused in particular by Woody Plant Encroachment (WPE), has been a common phenomenon in savanna ecosystems (Archer *et al*., 2017). During this process, woody thicket species, shrubs and trees increase in density and cover in open grassland (Van Auken, 2000; Ward, 2005). New thickets have been formed in savanna and woodland areas as a result of woody plant encroachment (Khavhagali and Bond, 2008). Generally, some areas experience successive transformation from grassland to woodland and, finally, forest, a phenomenon referred as forest colonization (Bond, 2008). Increased woody biomass normally comprises thorny and unpalatable species (Kgosikoma and Mogotsi, 2013), outcompeting and/or suppressing palatable grasses and herbs (Ward, 2005). Bush encroachment decreases herbaceous production and biomass, and in some cases increases species richness and diversity (Auken, 2009). As herbaceous production and biomass decreases, native plant seed rains become reduced, and natural storage of dormant seeds within the soil decreases with time (Saatkamp *et al*., 2014). When native species seeds become completely lost in the soil seed banks, the land loses its ability to regenerate native species on the soil surface (Yachi and Loreau, 1999). These changes may negatively affect grazing activities by reducing the quality and quantity of grazing land resources (Treydte *et al*., 2007), and consequently species community assemblage as well as ecosystem services to local communities.

In sub-Saharan Africa, woody plant cover has increased by 8%, i.e., 7.5 million km^2 from 1986 to 2016 (Venter *et al*., 2018). This increase likely decreases rangeland carrying capacity, i.e., quantity and quality (Karuaera, 2011; Venter *et al*., 2018), changing the vegetation structure from open grassland to scrubland. Eventually, encroaching woody plants might conduct self-thinning as a function of density at a certain point of time, i.e., seedlings will not grow and overall tree sizes and numbers will be reduced (Sea and Hanan, 2012). As encroached sites differ in plant community composition and/or structure due to intra and or inter-specific competition, there is a need to assess and quantify structural changes (Jurena and Van Auken, 1998; Venter *et al*., 2018) that may influence future woody plant encroachment of the site.

The impact of woody plant encroachment on herbaceous plants can be negative, neutral or positive, and depend on the abundance, growth form, root arrangements and canopy architecture of the encroaching woody plant (Archer, 1995; Eldridge *et al*., 2011). In North America, for instance, a woody plant increase in grassland has changed the plant community composition and reduced plant species richness (Eldridge *et al*., 2011; Ratajczak *et al*., 2012). Contrary to this finding, other studies have reported increases of herbaceous species, i.e. shade-loving herbaceous species under canopy of trees (Treydte *et al*., 2007; Wonga and Wilson, 1980), and/or defense mechanisms against grazers as they grow under thorn shrub of woody plant (Dharani, 2006).

Woody plant encroachment can lead to substantial changes of herbivore community assemblages in savanna ecosystems. Low herbaceous species cover due to woody plant encroachment decreases grazer species abundances and increases browsers (Smit and Prins, 2015). Encroached sites also create hunting cover for predators, creating a landscape of fear for medium-size herbivores such as zebra, hence woody encroached sites are mainly visited by mega-herbivores or large mammal species such as elephant that can feed on or alter woody vegetation (Smit and Prins, 2015).

The impacts of woody plant encroachment on herbaceous species are complex and can be difficult to identify. To understand herbaceous species composition under bush encroachment, soil seedbank analyses and field surveys of herbaceous species can be used. Studies on the soil seed bank of grazing land and intensively invaded land show unclear relationship between above-ground herbaceous species and soil seed bank species (Friend *et al*., 1997). For example, Jacobs and Richardson (2015) found that some plant species occurred only either in the soil seed bank or on top soil vegetation. Under the insurance hypothesis, there are relatively more or few unique native herbaceous species within the soil that might pop up once encroachment is cleared (Madawala *et al*., 2016).

Identifying optimum levels of disturbances i.e. rainfall, fire and grazing that influence savanna ecosystems dynamics is critically important to attain their management worldwide (Sankaran *et al*., 2004). Its argued that disturbances form part of savanna ecosystem, however under extreme condition may shift the stability state (tree-grass co-existence) of the ecosystem, consequently affecting ecosystem services i.e. grazing area, foods and medicines for society.

Tree-grass co-existence dynamics have also been discussed in framework of equilibrium, non-equilibrium and disequilibrium dynamics (Sankaran *et al*., 2004). In all equilibrium dynamics its appreciated that tree-grass ratio can fluctuate in response to both variable rainfall and disturbances such as fire and grazing (Sankaran *et al*., 2004). Plant germination and early seedling growth are highly susceptible to changes in climatic conditions, particularly water availability (O'Brien *et al*., 2013). However, little is known on how precipitation variation may influence seedling establishment that can consequently lead to woody encroachment. To fill such a gap this study experimentally observed the influence of precipitation on seedling establishment.

Another potential factor influencing seed germination and seedling establishment is consumption and seed gut passage by different herbivore species. Because animal dung represents a very different microclimate than soils (i.e., temperature, nutrients and moisture) seeds in dung may experience different rates of seed germination and establishment (Tjelele *et al*., 2015; Vega *et al*., 2010). While herbivore dung contains significant concentrations of nutrients, it retains heat and loses moisture more rapidly than soil, and thus may limit seed germination (Wilson and Witkowski, 1998). A third factor that can affect seed germination and establishment are bush fires, which are common in African savanna ecosystems (Calabrese *et al*., 2010; Frost and Robertson, 1987). Fires can directly kill seeds and seedlings, but it can also reduce grass abundance, thereby promoting tree seedling establishment indirectly by reducing competition from grasses.

To better understand the key processes, which control seed germination and seedling establishment, and their influence in promoting bush encroachment, we experimentally manipulated soil moisture, dung micro-habitat by herbivores and fire in a natural savanna setting. We conducted our work in a grassland of Maswa Game Reserve, which is located on the western side of the two major world heritage sites, Serengeti National Park (SENAPA) and Ngorongoro Conservation Area (NCA), and is an ecologically important area of the Serengeti ecosystem in Tanzania (Calabrese *et al*., 2010; Frost and Robertson, 1982). It's an important refuge and maternal site for wildebeest and other herbivore species in the Serengeti ecosystem (TAWA, 2016). Since 2011 open grassland areas have been increasingly encroached, mainly by *Acacia drepanolobium*. Increasing woody plant encroachment (Niboye, 2010) in open grassland affects forage availability by the herbivores, and raises concern over the rangeland quality and herbivore welfare in the Serengeti ecosystem.

1.2 Problem statement

Woody plant encroachment is one of the most widespread forms of land degradation in African rangelands and elsewhere (Archer *et al*., 2017). So far, its exact causes are still one of the least understood (Archer *et al*., 2017; Kgosikoma and Mogotsi, 2013), including synergetic interactions among several factors (Archer *et al*., 2017; Auken, 2009; Bond, 2008). There is a need for conducting experimental studies to find out how these multiple factors might interact and cause bush encroachment (Bond, 2008; Ward, 2005).

Encroachment of *Acacia drepanolobium* in Maswa Game Reserve is a mushrooming concern in wildlife conservation and a potential source for ecological and economic losses (Hopcraft, Personal communication, December 2017; Williamson, Personal communication February 2018). While the impact of bush encroachment has been investigated in various studies, little is known about why and how woody plant seedlings can so easily proliferate and spread and the role that wildlife and livestock play in this process. This study involved experimental as well as observational techniques to study the interactive role of herbivore-induced factors, fire and rainfall on facilitating encroachment of *A. drepanolobium* in Maswa Game Reserve, northern Tanzania.

1.3 Justification of the study

Management of wildlife habitat requires data and information to make informed decision of habitat intervention, specifically the invaded habitats. This study contributes to understand the impact and the contributing factors that influence bush encroachment in grassland areas. Such information can be used in restoration of invaded land, as well as prevention and or control of bush encroachment in grassland areas.

Savanna ecosystems and their processes are complex and rich in wildlife resources as well as human activities. Savanna management becomes difficult and complex due to synergetic interactions amongst savanna ecosystem components and processes. This study looked at the effect of fire, herbivores and rainfall regime on grass-tree co-existence.

There are limited studies in Tanzania on the driving factors of seedling establishment (Morrison *et al.,* 2019) and only few have conducted experimental tests of germination and seedling survival across the Serengeti rainfall gradient. Hence, this study contributed to understanding the factors that promote seedling emergence and establishment and, hence, tree recruitment processes in savanna systems.

Climate change, specifically rainfall variability, contributes to vegetation changes in savannas. Its predicted that rainfall patterns and amount will change due to climate change (Primack, 2010). However, it’s not clear how these rainfall changes might affect plant species, vegetation structure and, hence, the ecosystem at large. Using irrigation experiments, this study provides information on how rainfall variability facilitates seedling establishment.

African savannas often host *Acacia* species, woody plants that are leguminous and play a great role in nitrogen cycling as they are nitrogen fixers (Dharani, 2006). These tree species further support pollination of crops, erosion regulation and waste regulation (Hönigová *et al*., 2012). Some studies have shown that young tree species are not as beneficial in improving grassland quality compared with older and larger trees (Treydte *et al*., 2007). Hence, the bush encroachment, often dominated by small proliferating tree forms, threatens also the overall grassland quality. This study provides information that will contribute to the management of savanna, specifically earlier tree recruitment processes that can lead to changes of savanna vegetation structure.

1.4 Objectives

1.4.1 General objective

To quantify how bush encroachment influences the native plant species community and to identify the main factors promoting bush encroaching species’ seedling emergence and survival.

1.4.2 Specific objectives

(i) To assess the structure and diversity of native savanna plant communities under three different intensities of bush encroachment.

(ii) To examine the effect of dung (as a growth medium environment) and fire on seed germination of *A. drepanolobium.*

(iii) To examine the effect of rainfall variability patterns on seedling establishment of *A. drepanolobium*.

(iv) To assess spatio-temporal changes on vegetation cover in Maswa Game Reserve over a thirty-year period.

1.4.3 Hypotheses

H1: We expected that native herbaceous plant communities will show higher species richness and lower biomass in areas encroached by *A. drepanolobium*.

H3: Fire treatments will help in seed scarification and, in turn, enhance seed germination.

H4: Further, herbivore dung will provide less moisture for seedling germination compared to an environment without dung, i.e. soil watered daily, presenting typical wet season environment and, thus, higher germination rate.

H5: Tree seedling germination will be higher when abundant water is available to initiate the seedling emergence while a continuous lower water amount will be more crucial in the later stage of the seedling establishment.

CHAPTER TWO

LITERATURE REVIEW

2.1 Woody plant encroachment in savannas

Most studies on savanna ecology have investigated the contribution of land use and land use changes as well as disturbances i.e. fire, rainfall and herbivores on the encroachment of woody species (Stevens *et al*., 2016). Despite such efforts mechanisms regulating savanna tree populations are still not well understood (Holdo *et al*., 2009; Tefera *et al*., 2008).

Worldwide vegetation structures of savanna ecosystem are transformed from grassland to shrub land (Auken, 2000; Baez *et al*., 2012). In United States 19 million hectares of grassland has been transformed to shrubland. Shrubification is likely the results of multiple interacting factors in savanna ecosystem, and climatic variability is one among potential driver of tree-grass co-existence (Archer *et al*., 2017; Auken, 2000; Baez *et al*., 2012; Bond, 2008).

Almost eight (8) million km^2 of savanna has been encroached by woody plant in Africa (Venter *et al*., 2018), depleting rangeland carrying capacity and quality (Karuaera, 2011; Venter *et al*., 2018) and therefore these structural changes need to be assessed and quantified (Jurena and Van Auken, 1998; Venter *et al*., 2018). Effect of woody plant encroachment on herbaceous plants varies from negative, neutral and positive effect (Archer, 1995; Eldridge *et al*., 2011). Declining of herbaceous species cover due to woody plant encroachment decreases grazers abundances and increases browsers abundances, thus may have consequent effect on predators (Smit and Prins, 2015). Thus, woody plant encroachment leads to substantial alteration of community assemblage of herbivore and prey predator interaction in savanna ecosystem.

It has been found that soil moisture and plant biomass is function of precipitation, and therefore population and community structure are expected to be sensitive to rainfall variability and or patterns in the growing period (Reynolds *et al*., 2012). Shrub encroaching species are said to be more stable in production than grasses (Xia *et al*., 2010), hence impacting transition stages of grassland to bush-land (Muldavin *et al*., 2008). However, seedling emergence and establishment as critical stage in tree-grass co-existence has been poorly investigated under current and future climatic scenario.

For decades, wildlife resources and ecosystem function have been vulnerable and or altered due to climate change (Abdi *et al*., 2013; Archer *et al*., 2017; Kreyling and Beier, 2013; Walter *et al*., 2011). Precipitation and temperature have been widely studied climatic factors influencing flora and fauna species distribution, abundance and hence population and community structure (Zavalloni *et al*., 2008). Most precipitation studies have been designed as experiment to capture impact of rainfall on plants (Beier *et al*., 2012; Fay *et al*., 2000). However, in southern hemisphere and Africa in particular have been missing or lowly represented in these studies (Beier *et al*., 2012).

Acacia species are one of the least studied species despite being dominant in east Africa (Dharani, 2006). Soil seed bank and seed germination studies can highlight woody plant regeneration dynamics, but they have not often been studied in protected areas and their surroundings (Stelli, 2011). While a loss of woody plants in the Serengeti ecosystem has been described (Holdo *et al*., 2009), the woody plant encroachment of young seedlings has rapidly increased and is taking position over grasses in some parts of the Serengeti ecosystem. Little is known about the processes of seedling establishment and growth performance under various environmental and animal-induced factors.

Herbivores, specifically mega herbivores, have been found to play significant roles in the maintenance or changes of savanna structure as they can transform habitat through seed dispersal, reduce herbaceous biomass, hence indirectly controlling fire regime, and break large trees in woodlands, hence giving space for young woody and herbaceous plant to grow (Holdo *et al.*, 2009). Most encroached areas across African savannas have not been visited by African elephants (*Loxodonta africana*) (Stevens *et al.*, 2016), a fact which might have contributed to the often dense woody vegetation. The reported findings seem not to be applicable on Acacia encroachment in Maswa Game Reserve where the African elephants are inhabitants.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study area

The study was conducted from March to July 2018 within Maswa Game Reserve (Fig. 1), an area occupying 2200 km^2 within Serengeti ecosystem in Tanzania (TAWA, 2016; URT, 2017a). This area is an important shield for the Serengeti National Park and Ngorongoro Conservation Area (Chami, 2018; URT, 2017b), ecologically it offers maternity ground for wildebeest during dry season and part of great wildebeest migration in Serengeti-Maasai Mara ecosystem (TAWA, 2018). It's found in longitude 34^0 35' 49.6" E and latitude 3^0 17' 3.7" S (TAWA, 2018). Here, illegal livestock incursion inside the reserve has been serious problem. Main wildlife species present include giraffe (*Giraffa camelopardalis*), wildebeest (*Connochaetes taurinus*), waterbuck (*Kobus ellipsiprymnus*), African elephants (*Loxodonta africana*), buffalo (*Syncerus caffer)*, impala (*Aepyceros melampus*), topi *(Damaliscus korrigum)*, zebra (*Equus quagga*), baboon (*Papio anubis*), and variety of antelopes and bird species, jackal (*Canis aureus*), hyena (*Crocuta crocuta*), leopard (*Panthera pardus*), and lion (*Panthera leo*) (TAWA, 2016; URT, 2017a). Vegetation of the area includes Acacia woodland, thorn scrub, short grass plains, grassland areas and Kopjes (URT, 2017b). Maswa Game Reserve, just like other parts of the Serengeti ecosystem, has two wet seasons, i.e. short rains and long rains with rainfall ranges of 600 to 900 mm per year (Bartzke *et al*., 2018; URT, 2017b). Its average temperature follows within that of Serengeti ecosystem i.e. 9°C to 22°C in winter season, and 18°C to 31°C in summer (URT, 2017b). Maswa Game Reserve found in Simiyu region, and its bounded within Bariadi, Itilima and Meatu districts (Chami, 2018). The main ethnic group of the area includes pastoralists groups, farmers and hunters mainly from Sukuma tribe (Chami, 2018; Jangu, 2012). For the past two decades the grassland areas in Maswa Game Reserve have been changing, with *Acacia drepanolobium* increasing and becoming dominant (Niboye, 2010).

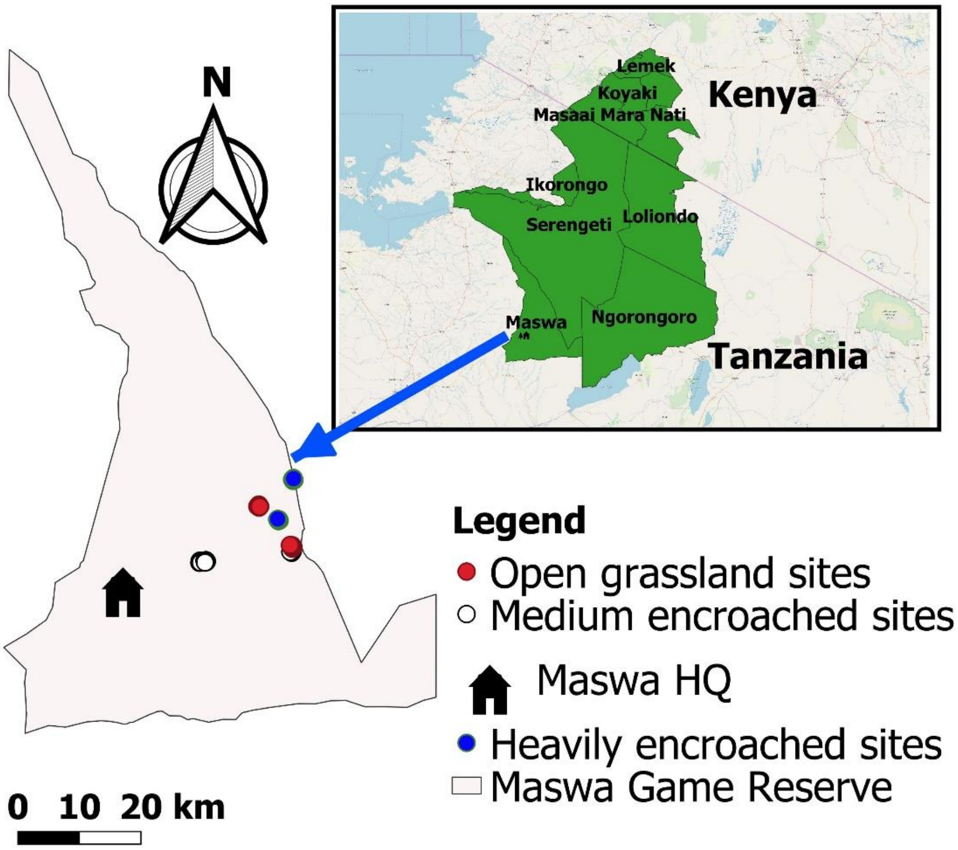


Figure 1: Study sites in Maswa Game Reserve, northern Tanzania. The house represents the Game Reserve headquarters (HQ) while circles represent study site locations of different woody density, Open grassland = sites with no encroachment, medium encroached sites = sites with less than 50% of woody cover, heavily encroached sites = sites with more than 50% of woody cover.

In Maswa, the mean annual precipitation over the past eight years was 663 ± 26 mm with most rain falling from January until May (Fig. 2). During this period, the years 2010 and 2013 had higher rainfall (wet), while the years 2011, 2012, 2014, and 2015 had lower rainfall.

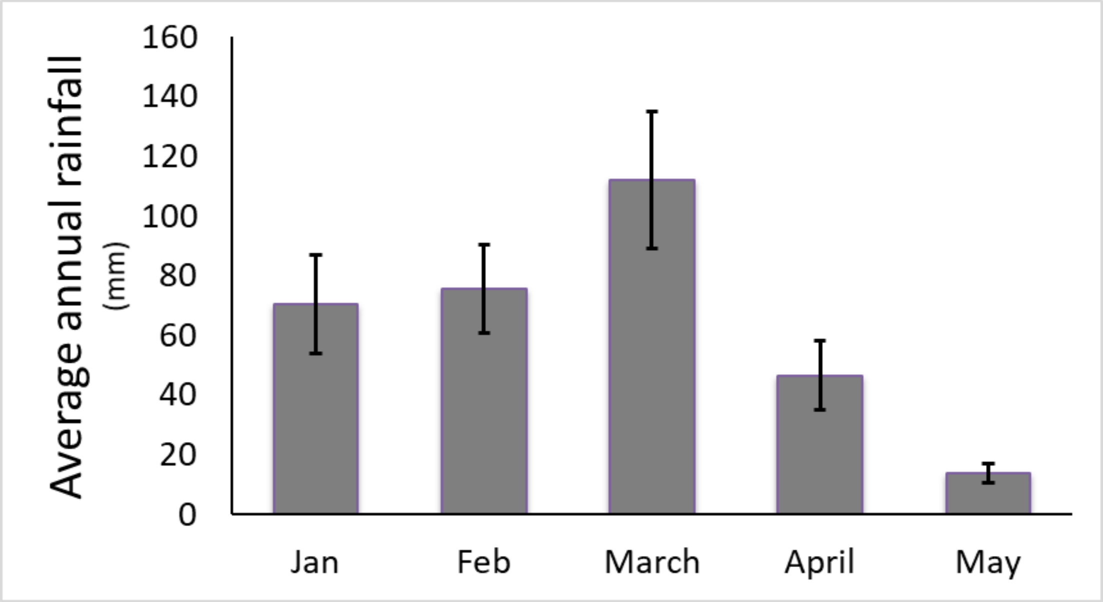


Figure 2: Average (±SE) annual precipitation (in mm) over the long rainy season in Maswa over the years 2008 until 2015. Source: Maswa Game Reserve headquarter.

3.2 Sampling design

Forty-four 400 m long transects, each containing four plots i.e. making a total of 192 plots were established over six sub-sites within (Fig. 1) the study site (Buckland *et al.*, 2007). Transects were placed 50 m apart from each other, and in total we covered 96 000 m^2 in all six surveyed sites. Transects were stratified by encroachment category, which were defined by visual assessment (Beltrán, 2015). Sixteen transects, comprising 64 plots each, were located within each an established encroachment category, i.e. (1) heavily encroached (>50% bush cover), (2) moderately encroached (< 50% bush cover), (3) no encroachment (no bush cover but only sparse trees and continuous grass cover (Beltrán, 2015). In each of the three encroachment categories, direct and indirect (e.g. dung piles, foot print and forage activity) observations of large mammal occurrence (carnivores, browsers and grazers) were assessed within four 10 x 10 m plots (Bacaro *et al.*, 2015), located every 100 m along the transect (Keeping and Pelletier, 2014). We could not count dung and track occurrences because of rainfall that destroyed tracks and signs, thus we recorded presence/absence data only. The dung, footprint, and forage activity reflected the relative use and/or access of the encroachment category by herbivores (Pfeffer, 2016). Along each transect, encroaching trees were identified and counted in plots and bare ground cover was visually estimated (Monteiro *et al.*, 2018). Multi-stemmed woody plants were considered as separate individuals if they were >40 cm apart (Tefera *et al.*, 2008). Data obtained were used in analysis of abundance, structure and composition of woody plant species. A plot of 1 x 1 m in size was established at the NE corner within each of the 10 x 10 m plot, and herbaceous vegetation cover was visually estimated for each identified plant species (Damgaard, 2014). Woody plant structure (canopy diameter, stem diameter at 1 m height, seedling occurrence, and height) was also recorded. All 10 x 10 m plots along each transect were categorized into lower slope plots (n = 32) and upper slope plots (n = 32) in heavily encroached site i.e. a gradient that water will move during rainfall (from upper slope to lower slope areas).

3.3 Irrigation experiment

Acacia drepanolobium pods (with an average weight 1.54 ±0.13 g) were collected from beneath *A. drepanolobium* trees in Maswa from June to July 2018. Only visibly healthy individual seeds were hand-selected and seed maturity was checked by opening 5-10 seeds and ensuring that the radicle was fully formed (O'Brien *et al*., 2013). Furthermore, seed health was checked by using water, i.e., seeds that sank in a basin of water were deemed healthy (O'Brien *et al*., 2013). In total, approximately 825 seeds were placed in germination trays filled with black cotton soil (clay soil), collected from *A. drepanolobium* encroached sites, with 55 pots per tray and pot sizes of 5.2 × 5.2 cm (O'Brien *et al*., 2013; Wilson and Witkowski, 1998). Each tray was randomly assigned to one of three irrigation treatments (275 seeds per treatment) (O'Brien *et al*., 2013). Treatments were frequent (4 ml), Intermediate (9 ml), and Infrequent (30 ml) rainfall per pot for daily, two, and seven-day irrigation frequencies, respectively. These amounts represent precipitation variation patterns based on the overall annual precipitation for Maswa Game Reserve over the last nine years (Maswa Weather Station) and according to predictions by IPCC (Hulme *et al*., 2001). These watering regimes altered frequency while sustaining an approximately equal monthly rainfall range amount of 127 ± 19.1 mm, as is usually expected in March during the main rainy season. The frequent water treatment represented consistent low amounts of water available to seedlings per raining event, thus representing simulation of little drought stress as it occurs in the area. The intermediate treatment watering was done every two days, representing relatively more water at a time, thus, intermediate drought stress, while the infrequent watering treatment represented extreme rainfall conditions per raining event and high drought stress in between, following the established approaches (Nejad, 2011). Seeds were placed on their side on the soil surface to replicate natural seed position and pots were watered to saturation prior to planting. The germination trays were placed inside a wooden cage covered by a polythene net to provide slight shade and exclude rainfall and potential seed predators

(Fay *et al*., 2000; O'Brien *et al*., 2013). During the course of the experiment, average recorded temperature was 24.1^{o}C. Starting seven days after planting (Razeek *et al*., 2016; Wilson and Witkowski, 1998), seedlings were monitored daily for germination (radicle emergence), mortality and seedling development over 35 days, and seedling shoot height data were collected after every seven days. At the end of the experiment, total length of each seedling root and shoot was measured and recorded.

3.4 Large-mammal dung experiment

In total, 75 and 70 fresh (less than one-day old) dung piles of elephants (*Loxodonta africana)* and buffalo (*Syncerus caffer)*, were randomly located in the wild within the study site and five *A. drepanolobium* seeds were inserted in each dung pile, summing up to 375 and 350 seeds, respectively. The dung piles were then covered by thorny branches of *Acacia* and trees (forming 2 × 2 m cage) to prevent experimental set up destruction and deter seed predation by wild animal species. The set up was left in the wild under ambient temperature conditions (without extra water) and checked regularly over 14 days before data collection. As a control, a total of 385 seeds were collected from *A. drepanolobium* trees and planted in germination trays, watered (20 ml) daily over 14 days to resemble optimal wet season growing conditions. Data collected after 14 days included the number of seeds that germinated, as well as shoot and root heights of the seedlings that emerged within the dung piles.

3.5 Fire experiment

A total of 461 seeds from pods of *A. drepanolobium* were collected in the field which were subjected to three fire treatments i.e. cool fire (cool), hot fire (hot) and sub-soil fire (sub). The "cool" treatment encompassed 201 seeds that were placed on soil below grasses in a relatively (15 × 15 m) moist grassland patch (grasses still green), which was then ignited and burned for 30 min. For the "hot" fire treatment, 220 seeds were placed on soil below grasses in a relatively (15 × 15 m) dry grassland patch and burned for 30 min (grasses brown and dried). In the" sub" experiment, 40 seeds were placed in a thin sub-soil layer (0.5 cm deep), dry grasses were placed on top of it to form a quadrat of (90 × 70 × 25 cm) and burned for 10 min. After the fire had ceased, all seeds were collected from the soil and planted in germination trays, watered with 20 ml daily and monitored for seed germination over a period of 30 days. As a control, 220 seeds were planted in germination trays, followed by daily watering (20 ml) for 30 days. Seeds emerging from germination trays were counted and recorded.

3.6 Spatio-temporal changes of vegetation cover

Landsat images were used to analyze spatio–temporal vegetation cover changes i.e. average annual increases and decreases in woody cover in Maswa Game Reserve over three decades, following the methodology of Venter *et al.* (2018). One hundred GPS locations of areas with different vegetation cover were used as ground-truthing points. Supervised classification and maximum likelihood operation were used to generate vegetation cover maps. In addition, Normalized Difference Vegetation Index (NDVI) was applied to detect areas of vegetation cover increase or decrease. Layer stacking of band 4, 3 and for TM and ETM+ were done so as to recognize vegetation reflectance (Anderson *et al*., 2016). The images were classified to established vegetation classes for 1986, 2002 and 2018. Supervised classification and maximum likelihood operation were used to generate vegetation cover maps.

3.7 Data analysis

Analyses were performed using Microsoft excel for graphs, R environment for two-way ANOVA and Turkey HSD (v.3.4.1 The R Foundation for Statistical Computing 2017) and PAleontological STatistics (PAST) version 3.20 for Kruskal Wallis test, Dunn’s test, and Chi-square test (Hammer *et al.*, 2001). Data were checked for normality and for normally distributed data, two-way ANOVA was used to test for the difference in mean seedling shoot heights across three irrigation treatments over the five-weeks period. For non-normally distributed data Kruskal-Wallis test was used to test whether seedling root length differed across the three irrigation treatments. Dunn’s and Turkey HSD post hoc analysis were performed to test significant differences across means. We tested for difference of the number of successfully germinated seeds against planted seeds among treatments i.e. seed germination success in large-mammal dung piles and fire regime treatment using Chi-square test and binomial proportions test, respectively, at 95% confidence interval. Difference of number of trees, canopy diameter, average stem diameter, and number of sapling across encroachment intensity was tested using Kruskal Wallis followed by Dunn’s post hoc analysis to test for significant differences of values across encroachment intensity. In analysis of herbaceous species across encroachment intensity, we employed one-way ANOVA to test difference of number of herbaceous species across encroachment intensity, furthermore site similarity in terms of herbaceous species composition was performed using Bray Curtis similarity index and dendrogram for site similarity produced using PAST. A Kendall tau correlation that handle ties for non-normally distributed data was used to test for correlation of number of tree with sapling, canopy diameter and average stem size, additionally it was used to test a correlation with herbivores and herbaceous species (Hammer *et al.*, 2001).

CHAPTER FOUR

RESULTS AND DISCUSION

4.1 Results

4.1.1 Encroaching woody plant species

Across all encroachment categories we encountered a total of 818 stems of *Acacia drepanolobium, Acacia seyal* and *Commiphora africana*. On average, the heavily encroached sites had 1102 ± 82 stems ha^{-1} (Table 1), with *A. drepanolobium* dominating with (72%), while *C. africana* comprised 28%. Medium encroached sites had 327 ± 39 stems ha^{-1} (Table 1*),* with *A. drepanolobium* dominating with 44%, followed by *A. seyal* with (33%) and *C. africana* with 23%. Open grassland sites had 157 ± 30 stems ha^{-1} (Table 1*)*, with *A. drepanolobium* contributing 73% and *C. africana* 27%.

Table 1: Average (± SE) number of stems per hectare of the dominant tree species and associated encroaching tree traits across three encroachment categories in Maswa Game Reserve. Open grassland = sites with no encroachment, medium encroached sites = sites with less than 50% of woody cover, heavily encroached sites = sites with more than 50% of woody cover. Different letters show significant differences as per Dunn's post hoc test at 95% confidence interval.

	Open grassland	**Medium encroached sites**	**Heavily encroached sites**	X^2	***P***
stems ha^{-1}	157 ± 30^a	327 ± 39^a	1102 ± 82^b	51.7	<0.001
A. drepanolobium	128 ± 36^a	270 ± 29^a	860 ± 72^b	41.6	<0.001
C. africana	150 ± 50^a	280 ± 71^a	540 ± 70^b	59.5	<0.001
A. seyal	0^a	240 ± 34^b	0^a	37.3	<0.001
A. drepanolobium stem diameter	6.1 ± 0.92^a	6.8 ± 0.34^a	6.5 ± 0.15^a	1.9	0.39
A. drepanolobium crown diameter	2.2 ± 0.55^a	3.1 ± 0.18^b	3.2 ± 0.13^b	4.5	0.11
No of *A. drepanolobium* saplings	180 ± 24^a	240 ± 37^a	780 ± 66^c	51.7	<0.001
No of plots with *A. drepanolobium* seedlings	0^a	1^a	32^b	30.9	<0.001

Comparing heavily encroached sites in upper and lower elevations (implying direction of rainfall water runoff) we found that lower slope areas had a significantly higher number of *A. drepanolobium* stems than upper slope areas ($W = 669.5$, $P = 0.0345$, Fig. 3).

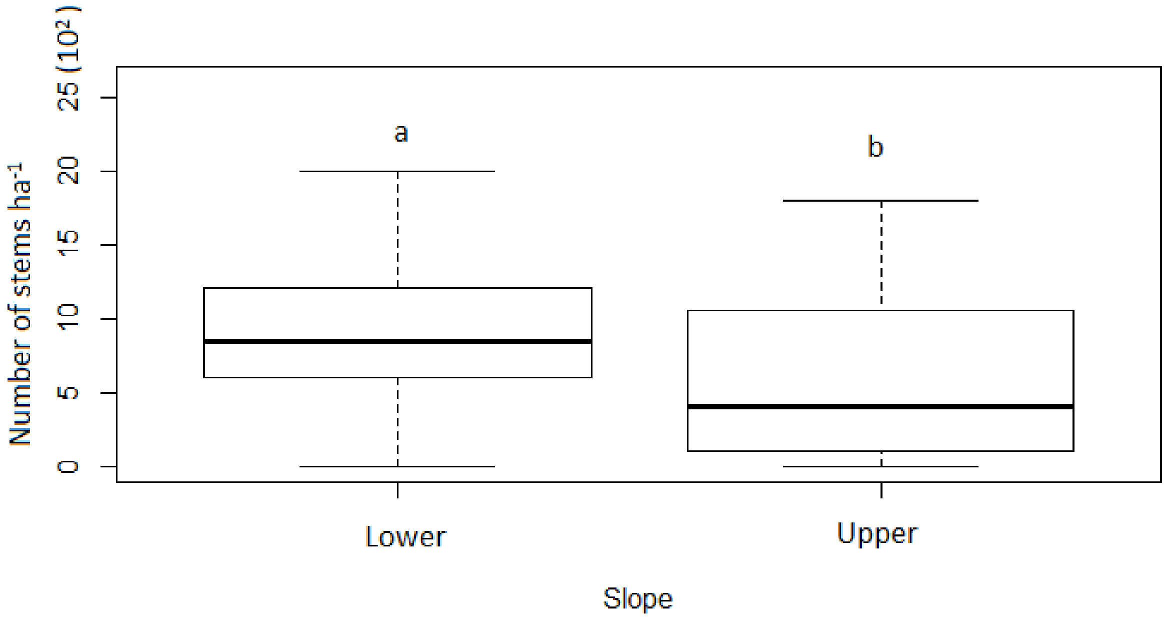
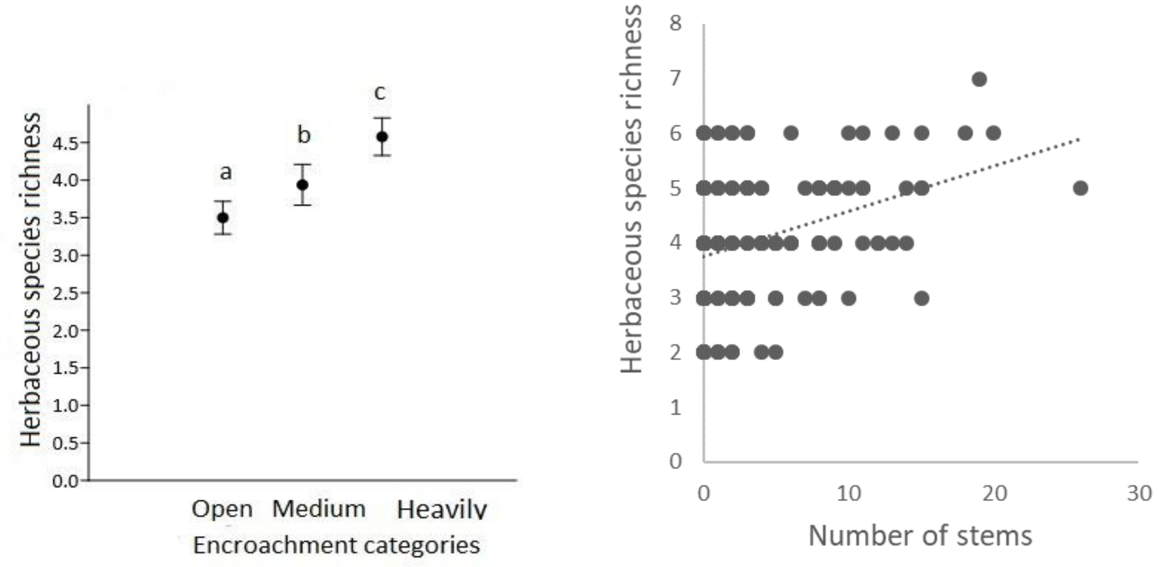


Figure 3: Median number of stems in lower slope area and in higher slope areas of heavily encroached sites only. Different letters show significant differences as per Wilcoxon signed rank test at 95% confidence interval.

Crown diameter differed significantly among encroachment categories and increased with higher encroachment ($X^2 = 69.08$, $P < 0.001$) as presented in Table 1. The average crown diameter in heavily and medium encroached sites was about twice as high compared to open grassland (Table 1), while *A. drepanolobium* crown diameter was only slightly higher in heavily than in medium encroached sites and both (heavily and medium encroached sites) were significantly higher compared to open grassland sites (Table 1). Average stem diameter did not differ across encroachment levels (Table 1). Sapling numbers of *A. drepanolobium* in heavily encroached sites were three times higher than those of medium encroached sites and four times higher than those of open grassland ($X^2 = 44.66$, $P < 0.001$) as presented in Table 1.

4.1.2 Herbaceous species and woody encroachment

The average herbaceous species richness differed slightly ($F_{2,189}$ = 18.39, P <0.001), showing on average about 1 species more at high encroachment levels (Fig. 4a).



4(a) 4(b)

Figure 4: a) Average (±SE) herbaceous species richness across encroachment categories. Open = no encroachment (grassland), medium = woody cover is less than 50%, heavily encroached = woody plant cover is higher than 50%. (b) Correlation of herbaceous species richness with number of stems across all encroachment categories. Different letters show significant differences in means according to Dunn's test at 95% confidence interval.

The number of herbaceous species increased slightly with increasing numbers of stems (r_7 = 0.24719, P < 0.001, Fig. 4b). The site similarity in terms of herbaceous species composition, revealed sites variation among encroached sites and non-encroached sites (Fig. 5).

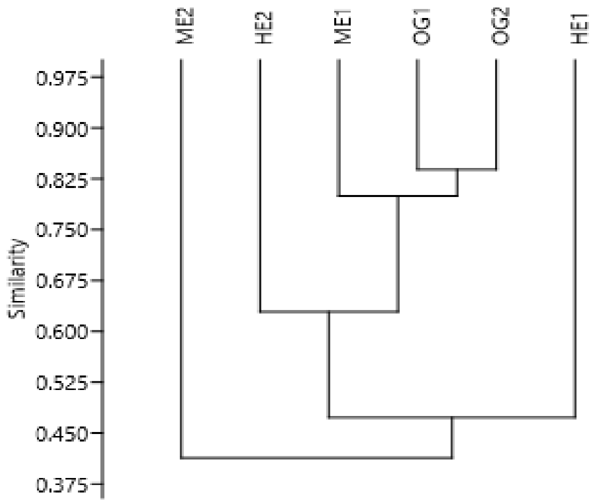


Figure 5 : Dendrogram for herbaceous species compositon similarity among encroahced and non encroached sites, Calculated using Bray curtis similarity index. HE1 = Heavily encroached site 1, HE2 = Heavliy encroached site 2, ME1 = Medium encroached site 1, ME2 = Medium encroached site 2, OG1 = Open grassland site 1 and OG2 = Open grassland site 2.

Inter-sites similarity was low for heavily encroached site 1 and medium encroached site 2 on one side with open grassland sites (Table 2). Additionally, medium encroached site 1 had high similarity with open grassland sites (Table 2).

Table 2: Bray Curtis similarity distances along encroachment categories, HE1 = Heavily encroached site 1, HE2 = Heavliy encroached site 2, ME1 = Medium encroached site 1, ME2 = Medium encroached site 2, OG1 = Open grassland site 1 and OG2 = Open grassland site 2.

	HE1	HE2	ME1	ME2	OG1	OG2
HE1	1					
HE2	0.47298356	1				
ME1	0.33123028	0.62879377	1			
ME2	0.26823529	0.36842105	0.41309431	1		
OG1	0.19212598	0.45221445	0.72926448	0.2692607	1	
OG2	0.18897638	0.47552448	0.79968701	0.35330739	0.8390625	1

In total, herbaceous species in heavily encroached sites are related to medium encroached sites by 47.9%, and to open grassland by 34%. However, herbaceous species in medium encroached sites are related to open grassland by 56%.

The average proportion of bare ground in open grassland differed significantly, with 2.7± 0.26%, while that of medium encroached sites was 9.1 ± 1.6% and that of the heavily encroached site was 18.1 ± 1.7% ($X^2 = 62.98$, $P < 0.001$, Fig. 6). Furthermore, the proportion of bare ground increased with increasing number of woody plant stems ($r_{\tau} = 0.38504$, $P < 0.001$).

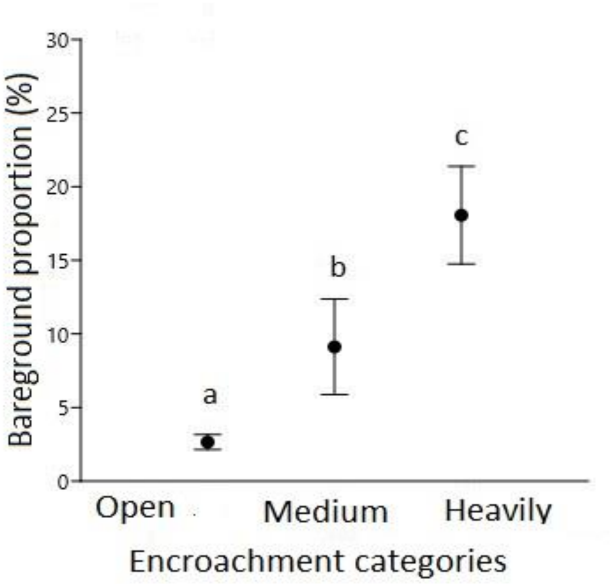
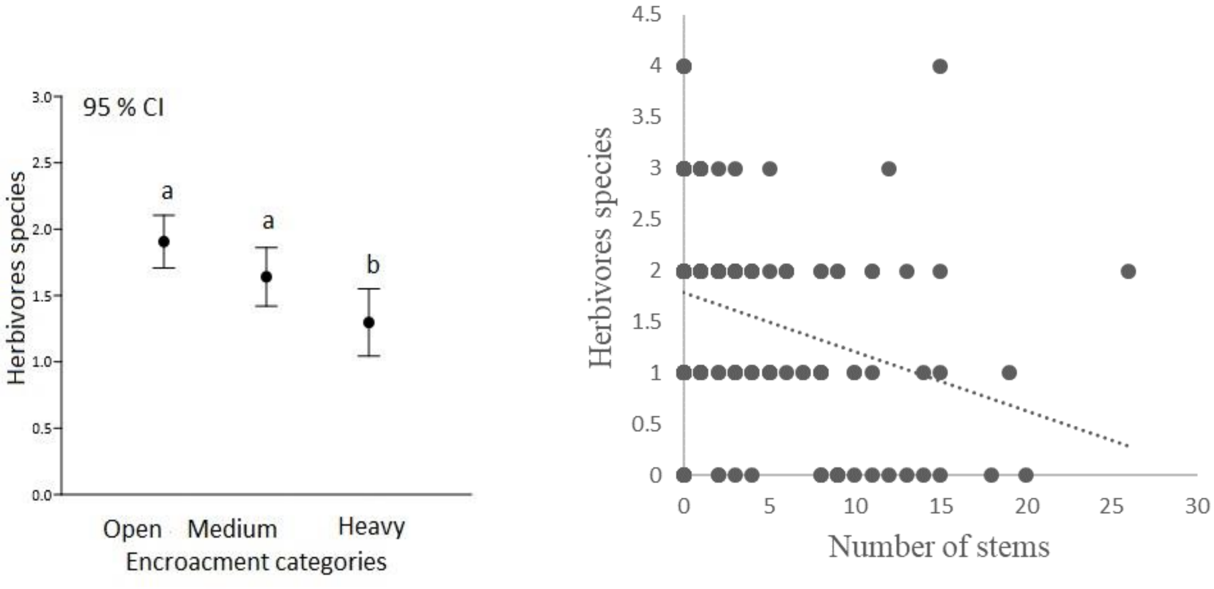


Figure 6: Average (±SE) proportion of bare ground across encroachment categories. Open grassland = sites with no encroachment, medium encroached sites = sites with less than 50% of woody cover, heavily encroached sites = sites with more than 50% of woody cover. Different letters show significant differences according to Dunn's post hoc test at 95% confidence level.

4.1.3 Herbivore species occurrence along encroachment intensity

The average number of herbivore species i.e. elephant, buffalo, giraffe, zebra, wildbeest, impala and dikdik, in open grassland and medium encroachment was two (2), while that of heavy encroachment was one (1) species only ($X^2 = 11.08$, $P = 0.002$, Fig. 7). Generally, number of observed herbivores species decreased with an increase in number of stems ($r_{\tau} = -0.204$, $P < 0.001$).



7(a) 7(b)

Figure 7: (a) Average number of herbivores species along encroachment categories (b) shows correlation of herbivores species with increasing number of stems. Open grassland = sites with no encroachment, medium encroached sites = sites with less than 50% of woody cover, heavily encroached sites = sites with more than 50% of woody cover. Different letters show significant differences according to Dunn's test at 95% Confidence Interval.

Table 3: The proportion of plots within which signs of different herbivore species/guilds were found (n = 64 per treatment) across each encroachment category. Different letters show significant differences as per Dunn's post hoc test at 95% confidence interval (N = 192).

	Open grassland	**Medium encroached sites**	**Heavily encroached sites**	X^2	***P***
Grazers	0.63^a	0.19^b	0.4^c	18.28	<0.001
Browsers	0.13^a	0.17^a	0.19^a	0.40	0.61
Mixed feeders	0.30^a	0.31^a	0.30^a	0.03	0.98
Predators	0.00	0.00	0.03		
Wildlife species:					
Loxodonta africana	0.16^a	0.19^a	0.20^a	0.22	0.78
Syncerus caffer	0.39^a	0.13^b	0.19^b	7.36	0.001
Giraffa camelopardalis	0.13^a	0.16^a	0.14^a	0.09	0.88
Equus quagga	0.30^a	0.08^b	0.09^b	5.25	0.002
Connochaetes taurinus	0.03^a	0.03^a	0.22^b	4.47	<0.001
Aepyceros melampus	0.13^a	0.17^a	0.11^a	0.40	0.56
Madoqua sp	0^a	0^a	0.05^b	0.28	0.005

4.1.4 Wildlife species occurrence with increasing number of tree cover

Generally, grazers species (wildebeest, zebra, buffalo) were negatively correlated with an increasing number of woody stems (r_T = -0.150, *P* = 0.002), browser (giraffe) was positively correlated with increasing number of stems (r_T = 0.05, *P* = 0.280) and mixed feeders (elephant and impala) were negatively correlated with increasing number of stems (r_T = -0.060, *P* = 0.200). Lion (*P. leo*) distribution was slightly positively correlated with increased numbers of stems (r_T = 0.120, *P* = 0.010). For herbivores species, giraffe was positively correlated with increased number of stems (r_T = 0.020, *P* = 0.770), while impala was slightly negatively correlated with increase of number of stems (r_T = -0.130, *P* = 0.080). Elephant and buffalo were negatively correlated with increasing of number of stems (r_T = -0.034, *P* = 0.489 and r_T = -0.082, *P* = 0.090) respectively. Zebra and wildebeest were negatively correlated with increasing number of stems ($r_{\tau} = -0.229$, $P < 0.001$, and $r_{\tau} = 0.120$, $P = 0.013$).

4.1.5 Seed germination under large mammal dung and fire treatments

Slightly but not significantly more seeds, i.e., 63 (17%) and 50 (14%) out of 375 and 350 seeds inserted in elephant and buffalo dung, respectively, germinated compared to the control 51 (13%) out of 385 ($X^2 = 2.009$, $P = 0.740$). Buffalo was only grazer species found abundantly in heavily encroached sites, and thus there is probability of seeds falling on buffalo dung or buffalo dung dropped on *A. drepanolobium* seeds. None out of 40 planted sub-soil hot fire treatment seeds germinated (Fig. 8), while in the hot fire experiment 5 (2%) out of 220 seeds germinated, in the cool fire treatment 3 (1%) out of 201 seeds germinated and in the control treatment 31 (14%) out of 220 seeds germinated ($X^2 = 37.692$, $P < 0.001$, Fig. 8).

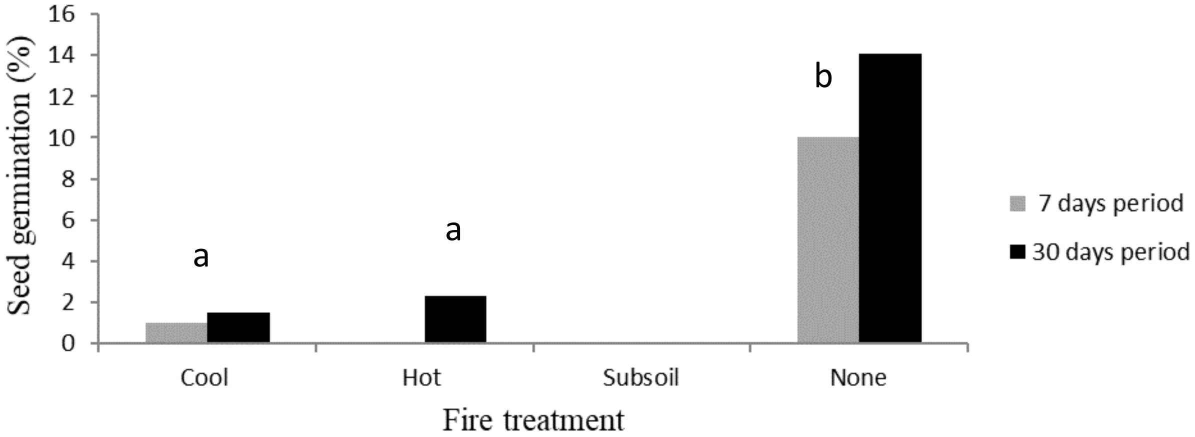


Figure 8: Seed germination (in %) of *A. drepanolobium* for different fire treatments over 7 days' (i.e., normal germination period; black bars) and 30-day period (i.e., the entire duration of the experiment; grey bars). Cool = green grassland patch was burned, hot = dry grassland patch was burned, sub-soil = seeds were located in 1cm depth within the soil, none = no fire. Different letters show significant differences according to binomial proportion test at 95% confidence interval.

4.1.6 Seedling growth under irrigation experiment

Across all three irrigation treatments, a total of 114 (14%) of all 825 planted seeds germinated within the five-week long experiment. Seed germination did not vary significantly among water treatments ($X^2 = 1.268$, P = 0.4091), with infrequent water treatment 37 (14%), intermediate water treatment 43 (16%) and frequent water treatments with 34 (13%) seeds germinating. Only the infrequent water treatment had 6 (16%) dying seedlings due to desiccation. Water treatments significantly influenced shoot height growth ($F_{2, 362} = 36.01$, $P < 0.001$) and significantly interacted with time on the influence of growth of shoots ($F_{6, 362} = 12.08$, $P < 0.001$, Fig. 9). Seedling shoots were slightly taller under frequent water treatment compared to intermediate water treatments, albeit not significantly (Tukey HSD Test: P = 0.059) while seedlings in frequent and intermediate water treatments were significantly taller than in the infrequent water treatment (Tukey HSD Test: $P < 0.001$).

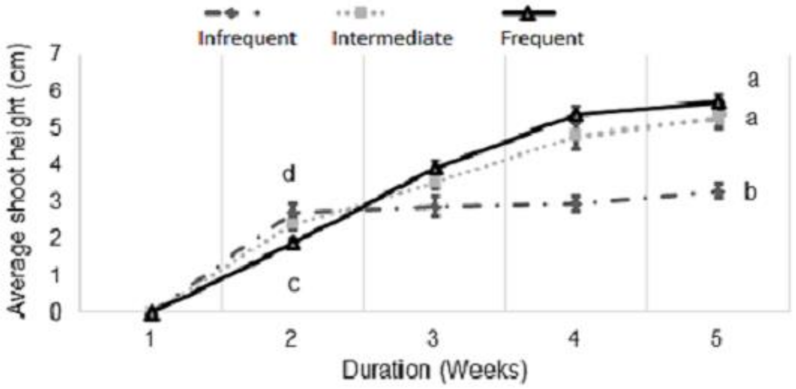


Figure 9: Average (±SE) seedling shoot heights over the entire duration of the experiment (five weeks) across three different irrigation treatments. High = 30 ml in seven days' period, medium = 9 ml in two days' period, low = 4 ml every day. Different letters show significant differences across treatments according to Turkey HSD at a 95% significance level.

Seedling shoot heights differed between the first week and fourth week, i.e., particularly seedlings of the infrequent water treatment did poorly as the experiment continued ($F_{3, 362} = 71.31$, $P < 0.001$, Fig. 9). Seedlings of infrequent and intermediate water treatment were about 1.4 times taller than frequent water treatment in the second week (Fig. 9). In contrast, at the end of experiment, the differences in seedling shoot heights among the treatments shows frequent and intermediate water treatment were almost twice as tall than infrequent water treatment (Fig. 9) while frequent and intermediate water treatment seedling shoot heights did not differ significantly.

Seedling root length after five weeks, i.e. at the end of the experiment differed significantly ($X^2 = 9.118$, $P = 0.0103$), with intermediate water treatment roots being almost twice as long as infrequent and frequent water treatment roots (Fig. 10).

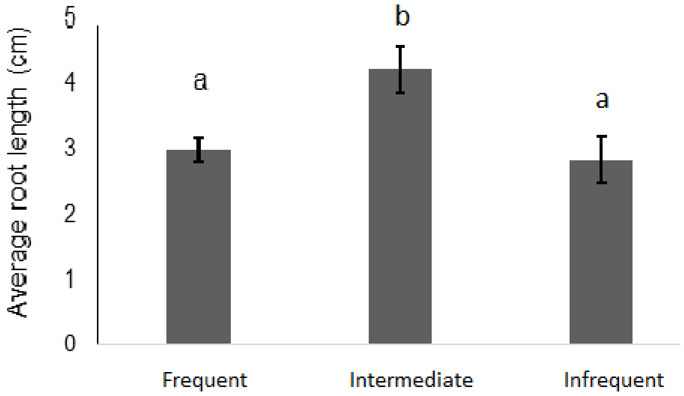


Figure 10: Average (±SE) seedling root length across irrigation treatments over a five-week period. Infrequent = 30 ml in a seven-day period. Intermediate = 9 ml in a two-day period, Frequent = 4 ml every day. Different letters show significant differences after Dunn’s Test and a significance level of 95%.

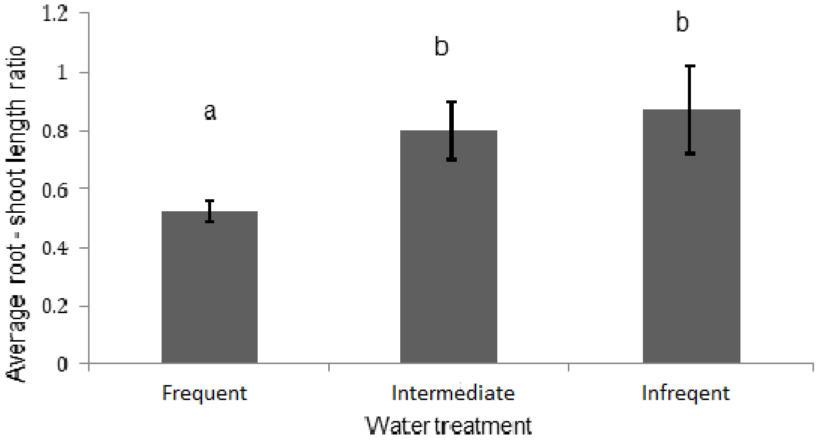


Figure 11: Average (±SE) root – shoot length ratio among irrigation treatment. Infrequent = 30 ml in a seven-day period, intermediate = 9 ml in a two-day period, frequent = 4 ml every day. Different letters show significant differences after Dunn's Test and a significance level of 95%.

4.1.7 Woody plant cover change

Woody cover from 1986 to 2016 decreased annually by 1.55% in the northern and southern areas of Maswa Game Reserve. While areas found in the middle of the Maswa Game Reserve experienced an average annual increase in woody cover from 1.55% to 2.63% (Fig. 12). The shrubland has increased by 932 km^2 (42.36 % of the current reserve area size) from 1986 to 2018 (Table 3). Generally, the increase of woody cover can be associated with an expansion of scrub land and shrubby grassland (Table 3).

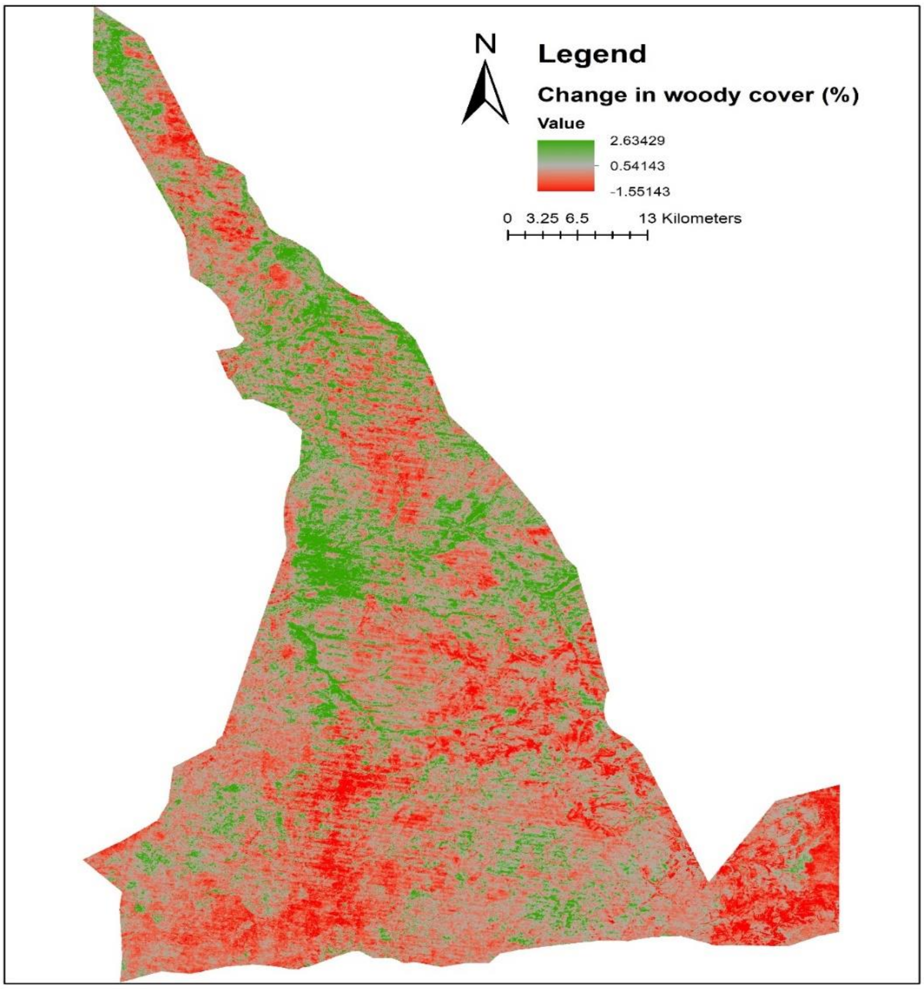


Figure 12: Average annual percentage change in woody cover from 1986 to 2016 in Maswa Game Reserve.

Table 4: Vegetation cover (km^2) changes in Maswa Game Reserve, vegetation changes from 1986 to 2018.

Class	**1986**	**%**	**2002**	**%**	**2018**	**%**
Water	0.0	0.0	0.0	0.0	0.0	0.0
Open Grassland	271.2	9.4	180.1	6.3	177.3	6.2
Shrubby grassland	619.6	21.5	884.7	30.8	473	16.5
Shrubland	67.4	2.3	247.9	8.6	999.4	34.8
Woodland	1897.2	65.9	1519.3	52.8	1155.1	40.2
Forest	22.3	0.8	14.2	0.5	3.2	0.1
Cultivation	0.0	0.0	27.1	0.9	52.8	1.9
Settlement	0.0	0.0	4.2	0.2	10.4	0.4
Total	**2877.8**	**100.0**	**2877.5**	**100.0**	**2871.2**	**100.0**

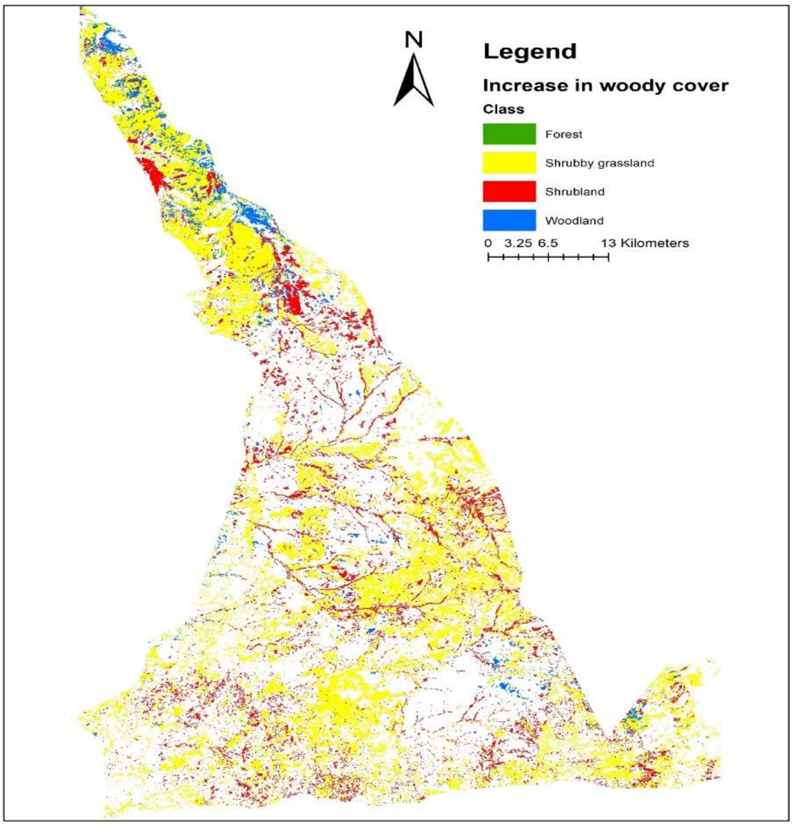


Figure 13: Areas converted to different woody cover vegetation forms from 1986 to 2018 in Maswa Game Reserve, white patches within the map present areas that retained their vegetation forms from 1986 to 2018.

4.2 Discussion

4.2.1 *Acacia drepanolobium* and *Commiphora africana* are the main contributors to bush encroachment

Our results suggest that *A. drepanolobium* is a major encroaching species dominating black cotton soil areas, followed by *C. africana*. Similar patterns have been found elsewhere (Angassa and Oba, 2007; Lemenih *et al*., 2011; Okello, 2007). *Acacia seyal*, in contrast, was a minor encroaching species. *Commiphora africana* was reported to encroach in other parts of Africa, while *A. seyal* was not found to be an encroaching species (Lemenih *et al*., 2011). The number of stems per hectare for all tree species combined in heavily encroached sites was three times higher than of medium encroached sites, and was seven times higher than that of open grassland. Despite the differences in number of woody plants along the encroachment intensity gradient, there were abundant saplings of *A. drepanolobium* in all encroachment levels, presenting the potential further increase of encroachment. Similarly, high numbers of *A. drepanolobium* saplings were reported by Lemenih *et al.* (2011). Such variation in woody cover affects wildlife species movement and habitat use, particularly in encroached sites (Smit and Prins, 2015), and thus impacts the ecological condition of grassland ecosystems (Yusuf *et al.*, 2011) and it jeopardizes tourism activities (Smit and Prins, 2015).

We found the level of encroachment impacted all tree size classes, heavily and medium encroached sites had both higher crown cover and higher seedling occurrence. In line with this result, Lemenih *et al*. (2011) reported a high seedling occurrence in encroached sites. In our study, open grassland lacked any tree seedlings. This could be a result of higher competition of water resources in open grassland due to higher grass cover in open grassland than in encroached sites (Morrison *et al*., 2019). Furthermore, mammal trampling and herbivore predation might also have suppressed tree seedling establishment in areas easily accessed by wildlife such as open grassland (Angassa and Oba, 2007).

4.2.2 Factors contributing to woody plant spread and encroachment

We found more trees per plot in lower slope areas than upper slope areas, probably highlighting the role of landscape topography in encroachment of *A. drepanolobium*. Initial woody plant encroachment has been found to be more significant in drainages within Serengeti ecosystem (Reed *et al*., 2009). Furthermore, lowland sites have high silt and clay content, and as these soils dry, they fracture and put stress on woody plants. However, *A. drepanolobium* has been shown to cope with this stress, whereas other woody plant species seem to be maladapted there (Pringle *et al.,* 2016).

In other parts of Africa, water has been suggested as dispersal agent of *A. drepanolobium* seeds (Lemenih *et al*., 2011). Additionally, in agreement with other studies, our result suggest woody plant encroachment may be highest in areas with low fire frequency and intensity. With increasing bare ground proportions, i.e. reduced herbaceous layer, in encroached sites, fire frequency and fire intensity also decrease (Reed *et al.*, 2009). Reduced fire intensity facilitates woody plant encroachment by increasing seedling and sapling establishment (Estes *et al*., 2008). Secondly, fire significantly reduces abundances of symbiont ants living on and in *A. drepanolobium* (Sensenig *et al*., 2017), which we also observed in our study (Personal observation, 2018). Reduced ant abundances in *A. drepanolobium* would weaken its defense against herbivores and increase access and or vulnerability to herbivory by herbivores, thereby hindering further bush encroachment. Because fire has been perceived to be destructive to habitat and to be detrimental to herbivores species, thus prescribed burning has been abandoned in most areas of Maswa Game Reserve since 2008. Preventing fire have been suggested to cause woody plant encroachment in other parts of Africa (Lemenih *et al.*, 2011; Yusuf *et al.*, 2011). The presence of mega-herbivores such as elephants may further contribute to spreading of *A. drepanolobium* (Brahmachary, 1980; Harich *et al.*, 2016; Nchanji and Plumptre, 2003). We found that, on average, one elephant dung pile carries 204 ± 14.84 seeds of *A. drepanolobium* (un-published data), a similar value of woody plant seeds per elephant dung found in Congo (Brahmachary, 1980). Furthermore, from our complementary experiment and field observations, *A. drepanolobium* seeds are capable of germinating in zebra, elephant and buffalo dung. When elephants shift from grazing to browsing in the hot dry season (August-October) in Maswa Game Reserve, they feed mainly on *A. drepanolobium* trees, including their pods and spread the seeds (Personal observation, 2018). Lastly, poaching of elephants could contribute to increases in woody cover as elephant tend to push over large trees and, thereby, open up woody area (Dempewolf, 2007; Stevens *et al.*, 2016). Over the last decade, Maswa Game Reserve has experienced rampant elephant poaching for ivory that lead to significant decreases in the local elephant population and had shifted their habitat to safer sites inside the Serengeti National Park (un-published data). Such shifts in habitat and decreases in elephant densities reduce browsing pressure and consequently enhance woody plants and the directional succession towards bushy vegetation (Dempewolf, 2007).

4.2.3 Woody plant encroachment trend with herbaceous species richness and bare soil cover

Increase of woody plant cover increased herbaceous species richness and bare ground proportion, thus encroached sites had slightly higher species richness of herbaceous plants of low herbaceous cover as predicted in our hypothesis. A study from southern Ethiopia reported a negative correlation between bush cover and grass cover, as well as positive correlation between bare soil and bush cover (Oba *et al.*, 2000). In agreement with our findings, Dharani (2006) indicated that *A. drepanolobium* covered sites harbor more species of herbaceous plants as it offers protection against herbivory. Open grassland sites had the highest scores of Bray Curtis similarity index (84%), a pattern that contrasts medium and heavily encroached sites similarities.

4.2.4 Woody plant encroachment slightly reduces herbivore species presence

Grazers' occurrence was slightly higher in open grassland than in medium and heavily encroached sites. However, grazer presence was also higher in heavily encroached sites than in medium encroached sites. Similarly, Okello (2007) reported herbivore numbers in *A. drepanolobium*-dominated vegetation was relatively low than in open grassland areas. In our study, browser occurrence was positively correlated with woody plant encroachment, while heavily encroached sites had the highest presence of browsers. Similar pattern for grazers and browsers correlation with bush cover were found in South African savannas (Smit and Prins, 2015).

Grazers and mixed feeders species were negatively correlated with increasing encroachment intensity, in contrast to browser species. Generally, we found fewer dung and track signs of herbivores in encroached sites than in open grassland. Lower herbivores species activities and loss of herbivores species in encroached sites may be a consequence of reduced habitat quality related to poor grazing opportunities, poor access due to thickets that hinder wildlife species movement and an increased landscape of fear due to higher predation rates (Pringle, 2018).

4.2.5 Seed germination and seedling growth under irrigation treatment

Our intermediate water treatment had the highest seed germination success, which might have been enough water to mechanically break the seed coat/wall i.e. regular contraction and expansion of seeds due to water absorption in a short period of time (Schopfer, 2006; Steinbrecher and Leubner-Metzger, 2016). Seed germination success of *Acacia tortilis* and *Acacia robusta* was found to be a function of rainfall in Serengeti (Morrison *et al*., 2019). In a similar study by Wilson and Witkowski (1998), comparable patterns of water treatment resulted in higher seed germination of *Acacia karoo* and suggested certain patterns of water availability causes loss of *Acacia* seed viability (Wilson and Witkowski, 1998). In other studies, intermediate moisture stimulated seed germination, presumably because too little water limited germination and too much water inhibited germination (Razeek *et al*., 2016). Our results emphasize the importance of consistency of soil water availability for *A. drepanolobium* seed germination.

In our study, seedling shoot heights were highest in frequent low water treatments over time except within the first week of treatment. Similarly, dry conditions rather than wetter conditions have been found to be beneficial for seedling establishment in Serengeti (Morrison *et al*., 2019). In addition, our results suggest that frequent low rainfall events are more important for seedlings than the actual amount of water supplied, in agreement with (Ferreira *et al*., 2015; Wilson and Witkowski, 1998). Thus, in addition to changes in total precipitation, changes in the temporal distribution of rainfall events may also influence germination success and establishment of *A. drepanolobium* seedlings.

While it has been reported that under limited resources, plants are able to alter their growth patterns by investing particularly in root growth (Bouteillé, 2011), we found shortest roots under frequent low rainfall treatment and root-shoot length ratios increased from low water treatment to high water treatments, i.e., the plants did not seem stressed (Harris, 199). Hence, we suggest that *A. drepanolobium* seedlings are sensitive to water availability, and can easily adapt to water stress situations within a short period of time. In Maswa, the year 2012 had the lowest rainfall records of all years, and during 2012 a wide establishment of *A. drepanolobium* saplings seemed to have taken place in the grasslands (un-published data). These findings are advocating for the role of bottom up process in regulating tree-grass co-existence, which is in line with studies on the role of rainfall in driving grass productivity in the Serengeti ecosystem (Coughenour *et al*., 1985) as well in other savanna ecosystems in the world (Fensham *et al*., 2005), particularly in the absence of fire (Jager, 1982).

Our field observation during the experiment and survey showed that water was readily absorbed and disappeared from the topsoil, which was mainly black cotton soil with deep wide cracks. Woodland and grassland distribution are correlated with infiltration rate and depth of soil moisture (Jager, 1982). Infiltration is positively influenced by deep wide cracks in the soil, with more moisture being available in deeper soil than upper soil (Jager, 1982). Thus, more water will be readily available to woody plant saplings rather than grasses, which use the upper soil layer for water acquisition (Sankaran *et al*., 2004). Previous findings suggest that soil types influence seed germination and seedling establishment of *A. drepanolobium* (Okello and Young, 2009; Okello, 2007), we observed that most *A. drepanolobium* encroachment sites were located in black cotton soil (Personal observation, 2018). It has been found as these soils dry, they fracture and put stress on woody plants. However, *A. drepanolobium* has been shown to cope with this stress, whereas other woody plant species seem to be maladapted there (Pringle *et al*., 2016). Further studies should focus on soil types as it could help in further understanding and prediction of woody encroachment.

4.2.6 Bush fire suppress *Acacia drepanolobium* seeds germination success

In addition to rainfall, fire is one of the major regulatory mechanism shaping vegetation structure and composition in savanna ecosystem and Serengeti in particular (Beale *et al.*, 2013; Strauch and Eby, 2012). Our fire experiment showed that seedling germination was reduced by 13%, which is in accordance with Okello (2007), who showed that fire significantly reduced seed germination success of *A. drepanolobium* in Kenya. In our study, cool fire, hot fire and subsoil hot fire treatments all suppressed germination of *A. drepanolobium* seeds, thus highlights that timing and duration of fires play an important role in shaping savanna vegetation. Seasonal prescribed fires are usually a management tool in protected areas and Serengeti-Maasai Mara ecosystem in particular (Dempewolf, 2007), but reduced bush fires experienced in some parts of Maswa could have led to bush encroachment as mentioned by Lemenih *et al.* (2011) and Yusuf *et al*. (2011) in Ethiopia.

4.2.7 Seed germination and seedling development under large mammal dung

Our results show that seed germination success in elephant and buffalo dung was not statically significant compared to the control. In Cameroon, a similar study reported fast seedling growth in elephant dung than in soil (Nchanji and Plumptre, 2003). Wickens (1969) suggested seed germination is more favored in fibrous dung due to lower nitrogen content, which explains our relatively higher germination success in elephant dung than in buffalo. Up to 100 seedlings has been reported to germinate per elephant dung pile (Brahmachary, 1980). Our germination experiment results suggest that seed germination in dung can happen independently of season if seeds grow in an advantageous environment such as large mammal dung piles. From our un-published data, on average one elephant dung pile carried 204 ± 15 seeds of *A. drepanolobium,* similar to findings by Brahmachary (1980), highlighting the potential role of elephants as seed dispersal agent (Harich *et al*., 2016; Lieberman *et al*., 1987).

4.2.8 Change in woody plant cover

South, west and north of the Maswa Game Reserve has experienced decreasing in woody plant cover, similar trend in decrease of woody cover has been reported by Homewood *et al.* (2001) and Dempewolf (2007). Decrease in woody plant cover has been found to be associated with storing fire intensity (Dempewolf, 2007) and increase in local human population (Makacha *et al*., 1982; Venter *et al.*, 2018), thus increase of pressure over natural resources i.e. land for settlement, cultivation, illegal fire woody and wood harvesting, as well as weak law enforcement especially in north of the park (un-published data). Our result, show more woody plant encroachment in east side of the Maswa Game Reserve i.e. peripheral boundary of Serengeti National Park and middle of the Maswa Game Reserve, Similar patterns on increase in woody plants has been reported by Homewood *et al*. (2001) in Serengeti ecosytem. Despite general change in woody vegetation classes, only shrubland had net gain i.e. increase in woody cover, and was highly pronounced in different areas of the Maswa Game Reserve from 1986 to 2018.

CHAPTER FIVE

CONCLUSION AND RECOMMENDATIONS

5.1 Conclusion

We found that in Maswa Game Reserve, *A. drepanolobium* was the main encroaching species in open grassland area, followed by *C. africana*, while *A. seyal* has been a least encroaching species. Based on our experiments and observations, fire suppression, elevation, large mammal dung and dispersal of the seeds by mega-herbivores might have been the most important factors supporting the spread and favorable growing environment of *A. drepanolobium* in Maswa Game Reserve. Encroachment of *A. drepanolobium* results in lower herbaceous cover, and a slight increase in herbaceous species richness. On the other hand, woody plant encroached sites hosted only few herbivore species compared to open grassland area. Grazers and mixed feeder species were negatively correlated with increasing woody density, while browsers and mixed feeders i.e. the giraffe and elephant, respectively, was positively correlated with increasing of woody plant cover. We found that fire treatments can strongly reduce germination success of *A. drepanolobium* seeds. In addition, large mammals might play an important role in seed germination and initial seedling establishment. We also found that minimal rainfall will lead to less successful seed germination but will positively support the growth of already established seedlings. Management has to take prescribed fire as well as mechanical intervention such as timely uprooting into account. The reported rainfall patterns in the long rainy season differed from those reported by Jager in 1982, thus suggesting a shift in rainfall patterns. These shifts in rainfall pattern could probably lead to a loss of tree-grass balance and, hence, to significant changes of vegetation structure in the long run.

5.2 Recommendations

Woody plant encroachment in wildlife habitat presents a potential ecological and economical problem for wildlife conservation. With increasing woody plant encroachment, the cost for intervening the problem will increase. We, therefore, recommend the following appropriate and timely actions:

(i) Systematic and appropriate measures to prevent further woody plant encroachment by clearing woody species mechanically in highly encroached areas. Cutting and burning for clearing woody plant encroachment of *Acacia zanzibarica* was done in Saadani National Park, and might help to successfully restore open grassland.

(ii) Fire management plan: prescribed fire burning in predefined locations, whereby timing and intensity of fire is very important.

(iii) Set up and use of experimental plot should be done during the restoration process to allow monitoring to reduce uncertainty in re-sprouting/seedlings success, to evaluate and improve restoration process.

(iv) We highly recommend further research on vegetation changes and or its impact on wildlife in Maswa Game Reserve, particularly on;

  a) How bush encroachment might impact predators and herbivore movement

  b) Remote sensing studies assessing woody vegetation change in more detail and monitoring on rainfall and temperature to understand correlations over time

  c) Soil studies and their influence on seed germination and seedling establishment

  d) Experimental removal/restoration plots for long-term monitoring on eradication success

(v) Ensure team work and stakeholders involvement amongst researchers, TAWA, TAWIRI, local communities, investors, TANAPA and academic institutions.

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