UNIVERSITY OF ZAMBIA

IMPACTS OF SHRUB ENCROACHMENT ON SOIL NUTRIENT PROPERTIES, PLANT DIVERSITY AND HERBIVORY IN LOCHINVAR NATIONAL PARK, ZAMBIA.

By

Griffin Kaize Shanungu

A thesis submitted to the University of Zambia in fulfillment of the Degree of Master of Science in Integrated Water Resources Management.

THE UNIVERSITY OF ZAMBIA

LUSAKA

2013

DECLARATION

I, Griffin Kaize Shanungu, declare that the work contained in this dissertation is my own work and that it has not been previously submitted for a degree or any award at this university or any other institution. All published work or materials from other sources incorporated in this report have been specifically acknowledged and adequate reference thereby given.

Student's signature…………………………………………………….

Date...

APPROVAL

This thesis of Griffin Kaize Shanungu has been approved as fulfilling the requirements for the award of the degree of Master of Science in Integrated Water resources Management by the University of Zambia.

Name and Signature of Examiners Date

1. Name ………………………………………………………… ………….

2. Name ………………………………………………………… …………..

External Examiner:………………………………………….. ……………

ABSTRACT

This study aimed at assessing impacts of *Dichrostachys cinerea* and *Mimosa pigra* encroachment on soil nitrogen, phosphorous and carbon pools as well as plant species diversity, vegetation composition and food supply for herbivores in Lochinvar National park of Southern Zambia. The study hypothesized that shrub encroachment a) increases soil nitrogen and carbon pools but leads to a reduction in soil phosphorous pools, b) reduces plant species diversity and changes the composition of the understory vegetation and c) reduces biomass production of the understory vegetation, and that this would lead to a reduction in food supply for large herbivores, particularly the Kafue Lechwe. In order to assess the impacts, 20 and 19 field plots were selected along gradients of increasing cover of *D. cinerea* and *M. Pigra* shrubs respectively in Lochinvar National Park. In each of the plots, soil samples were collected and measured for soil pH, bulk density and soil nitrogen, phosphorous and carbon pools. Nitrogen mineralization rate as well as nitrogen and phosphorous availabilities were also investigated. Plant species composition and biomass production were measured for each of the plots in the *D. cinerea* and *M. pigra* plots. The results of this study showed that encroachment of *D. cinerea* shrubs not only increased the soil pools of nitrogen and carbon linearly, but also that of phosphorous, whereas no such associations were observed in the *M. pigra* gradient. Furthermore, the encroachment of *D. cinerea* and *M. pigra* had significant impact on plant species diversity and richness and altered the understory vegetation composition. Both these encroaching species largely reduced cover of grasses and grass biomass production. This suggests that shrub encroachment had reduced food supply for grass-eating herbivores, particularly the endemic Kafue Lechwe, in Lochinvar National Park. These results as well as an analysis of shrub encroachment based on satellite images show that shrub encroachment had likely not reached its end yet, and hence might even further reduce the food for these herbivores in the future.

DEDICATION

To my parents Mr. and Mrs. Shanungu, my son – Nachiloba Shanungu – and my brother and sisters for their encouragement, love, patience and above all their prayers during the entire period of my research.

ACKNOWLEDGMENTS

I wish to thank the African Dams Project (ADAPT) – Zurich, Switzerland and Integrated Water Resources Management (IWRM) Center – UNZA, for their sponsorship, logistical and financial support throughout the duration of my research.

To my supervisors – Dr. Harry Chabwela, Dr. Harry Olde Venterink and Prof. Peter Edwards – I say thank you for your mentorship, guidance, support and comments on the drafts of this dissertation. My heartfelt gratitude goes to Dr. Harry Olde Venterink for always being professional and developing research skills in me. Thank you for your patience and friendship that you showed me through the years. I also extend my gratitude to Prof. Nyambe for his encouragement.

I thank Gerard Ellenbroek and Mike Bingham for their help with identification of plant species in the research sites. I extend my heartfelt appreciation to all the Zambia Wildlife Authority staff at Chilanga particularly Chuma Simukonda for their support during the period of my studies. And at Lochinvar National Park especially my trusted friend Benjamin Wishikoti, I say 'thank you' for your willingness and cooperation in all the fieldwork that we did and putting up with me during those long field excursions.

My everlasting gratitude goes to Wilma Blaser whose support and encouragement kept me motivated throughout the study. I thank you also for your friendship during my stay in Switzerland.

There are many people that I would like to thank for various reasons relating to this study. To those whom I did not mention, but who have assisted in some way, shape, or form, I am sorry not mentioning you by name, but am none-the-less grateful for your help.

Finally I would like to thank the Almighty God for having made it all possible.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER ONE: INTRODUCTION

1.1 Background

Over 40 % of the Earth's land surface is grassland, representing the largest biome of the world with an estimated area of coverage of 52.5 million km² (White et al. 2000). Evidence is accumulating of a general increase or encroachment of woody plants into grasslands, and the conversion of many grassland savanna regions of the world into shrub lands (Archer et al. 1995; Van Auken 2000; Van Auken 2009; Eldridge et al. 2011). Savanna grasslands are dynamic ecosystems composed of grass and woody plant species and are characterized by the apparent maintenance of the tree to grass ratio. This is maintained by complex interactions between edaphic factors, rainfall limitation and disturbance regimes such as herbivory and fire (Coetzee et al. 2006). A dynamic shift in any of these factors will change the maintenance of the grass to tree ratio and may lead to the conversion of one or the other state (Coetzee et al. 2006; Archer et al. 2000). The increase in density, cover and biomass of woody plants (typically trees and shrubs) into previously grassland-dominated areas is termed as shrub encroachment (Archer et al. 1995; Van Auken 2009).

Consequences of shrub encroachment on ecosystem functioning can either be negative, positive or neutral (Eldridge et al. 2011). Encroachment of shrubs in grassland savannas can lead to a reduction in their grazing carrying capacity subsequently affecting wildlife and the sustainability of subsistence and commercial livestock grazing (Archer et al. 2000). Shrub encroachment may also have significant consequences for biodiversity and ecosystem functioning (Eldridge et al. 2011; Van Auken 2009).

The grasslands of Kafue flats in Southern Zambia (Figure 1) have experienced significant encroachment of shrubs (Thomas 2007; Genet 2007; Blaser et al.

unpublished). The Kafue Flats are a rich mosaic of lush floodplain grasslands and lagoons sustained by the seasonal floodwaters of the Kafue River. The Kafue Flats are important as they provide habitat to the endemic Kafue Lechwe (*Kobus leche kafuensis* Gray, 1850) and the largest concentration of the threatened Wattled cranes (*Grus caranculatus* Gmelin, 1789) in Africa. Two National Parks lie in the Kafue Flats – Lochinvar and Blue lagoon as well as the Kafue Flats Management Area, which covers much of the Kafue Flats (Figure 1). The site is also designated as a RAMSAR Site, a wetland of International Importance under the Ramsar Convention. Since the early 1980s, the floodplain and adjacent termitaria grassland of the Kafue Flats, especially at Lochinvar National Park (LNP), had experienced significant shrub encroachment (Genet 2007; Thomas 2007; Gylstra 2009). This shrub encroachment is mainly attributed to changes in the natural cycle of yearly flooding after the construction of the Kafue Gorge Dam in 1972 and the Itezhi Tezhi Storage dam in 1978 on the Kafue River, for hydroelectricity generation (Genet 2007; Mumba and Thompson 2005; Gylstra 2009; Thomas 2007). Shrub encroachment on the Kafue Flats has been a major concern for conservation managers. Thus, understanding the problem of shrub encroachment on the Kafue Flats is one of the main technical challenges for sustainable environmental management. The main species causing the encroachment in the Kafue Flats are the native *Dichrostachys cinerea* (L.) Wight *et* Arn and the invasive *Mimosa pigra* L.

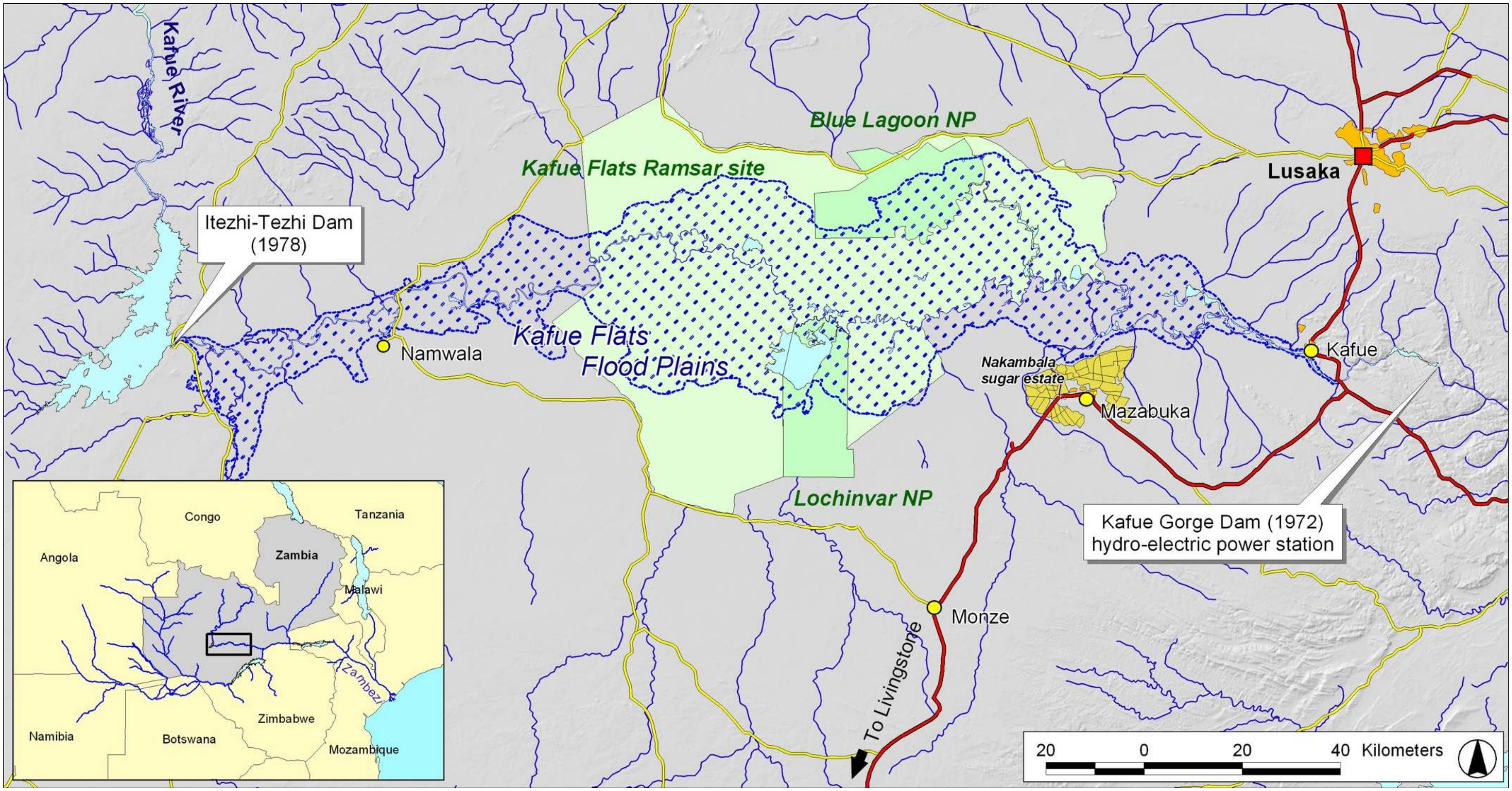

Figure 1: Location of the Kafue Flats Floodplains, Zambia (Source: Shanungu, 2009).

Mimosa pigra is a spiny leguminous shrub from South America that has become invasive in several parts of Asia, Australia and Africa, forming thick, impenetrable, one-species stands that exclude other plants and most animals (Lonsdale 1989; Paynter et al. 2000). *Dichrostachys cinerea* is a leguminous shrub, native to southern and central Africa and is one of the major encroaching species in grasslands in this region (Roques et al. 2001; Hagenah et al. 2009). These encroaching shrubs are occupy a significant proportion of the floodplain and termitaria grasslands in Lochinvar National Park (Genet, 2007). Both species have significant negative impacts on habitat and breeding cycles of some mammal species, biodiversity, tourism, and floodplain use by wildlife, livestock and fisheries (Chabwela and Mumba 1998; Kampamba and Nyirenda 2004). Even though the phenomenon of shrub encroachment and its impact on ecosystems has been widely reported (Eldridge et al 2011), empirical research exploring how specific ecosystems are impacted in terms of species diversity, plant biomass production and impacts on herbivory are still needed. In this study the impacts of *D. cinerea* and *M. pigra* encroachment on soil nitrogen (N), phosphorous (P) and carbon (C) as well as their impacts on plant species diversity and food supply for herbivores on the Kafue Flats floodplains were investigated.

1.2 Problem Statement

Recent studies on shrub encroachment in Lochinvar National Park (LNP) had focused on the spatial distribution and patterns of encroachment of the shrubs *M. pigra* and *D. cinerea* (Thomas 2007; Genet 2007). Other studies had shown how the encroachment of shrubs, particularly *M. pigra,* had negatively affected the diversity of bird species (Shanungu, 2009) and socio-economic impacts (Kampamba and Nyirenda 2004). Little, however, was known about how the encroachment of *D. cinerea* and *M. pigra* altered soil Nitrogen, Phosphorous and Carbon availabilities. Furthermore, little was known about how the encroachment of these shrubs had impacted on plant species diversity and food supply for herbivores, particularly the endemic Kafue Lechwe.

1.3 Objectives and Hypotheses

The overall objective of this study was to quantify how ecosystem properties (soil properties, plant species diversity, and biomass production) changed as the density of *D. cinerea* and *M. pigra* stands increased. The specific objectives of the study were:

1. To determine if shrub encroachment of *D. cinerea* and *M. pigra* altered soil nitrogen, phosphorous and carbon pools and availabilities, and other micro environmental conditions such as soil PH., bulk density, soil moisture and light.
2. To determine how shrub encroachment impacted plant species diversity and the understory vegetation composition of the encroached plant communities.
3. To investigate if shrub encroachment influenced food availability and quality for large herbivores (particularly Kafue lechwe).

The study tested the following hypotheses:

1. Shrub encroachment increases soil nitrogen and carbon pools but leads to a reduction in soil phosphorous pools.
2. Shrub encroachment reduces plant species diversity and changes the composition of the understory vegetation,
3. Shrub encroachment reduces biomass production of the understory vegetation, and that this would lead to a reduction in food supply for large herbivores, particularly the Kafue Lechwe.

1. 4 Significance of the Study

Lochinvar National Park is an important wildlife and bird sanctuary in Zambia. The study will yield important information on the impacts of encroachment of *D. cinerea* and the invasive shrub *M. pigra*, on soil nutrient properties, their consequences for biodiversity of the floodplain vegetation and herbivore food supply. These changes have important implications for local ecosystem dynamics and rangeland management. Hence, the results may be useful for Zambia Wildlife Authority and provide vital information in their attempt to control the spread of the invasive shrubs and conservation of biodiversity in Lochinvar national park and the entire Kafue Flats Floodplains. Furthermore, the information generated from this study could be useful in rangeland management for the pastoral industry. In addition, the study would add to a substantial body of literature of shrub encroachment in savanna ecosystems.

1. 5 Study Approach

The research involved a desktop study, field and laboratory work.

a) In the desktop study, a literature review was undertaken to document and understand previous research work on the impacts of shrub encroachment in grassland savannas in Africa and elsewhere.
b) Fieldwork was planned to investigate the impacts of shrub encroachment in the study area. It involved the setting up of plots and collection of field samples and various recordings on the selected plots for investigation.
c) Laboratory work was then done to analyse soil and plant samples collected from the field.
d) The collected data was analysed and interpreted.

CHAPTER TWO: LITERATURE REVIEW

2.1 Introduction

This literature review explores the impact of shrub encroachment on three main themes, namely, soil nutrient properties, plant species diversity and herbivory. While the impacts of shrub encroachment on these three main areas of ecosystem functioning is the scope of this particular study, this literature review is expanded to include research that also examines causes of shrub encroachment in grasslands in many parts of the world.

2.2 Shrub encroachment in grasslands.

Grassland savannas are extensive, socio-economically important ecosystems with a mixture of two life forms, trees and grasses (Scholes and Archer 1997), which are known to have strong interactions (Cabral et al. 2003). Historical evidence from the last 50 – 300 years suggests an increase in the surface area of woody patches in many grassland savannas (shrub encroachment) (Cabral et al. 2003). Shrub encroachment and the thickening of woody plant density in grassland savannas is rapidly occurring globally (Scholes and Archer 1997; Eldridge et al. 2011; Archer et al. 1995; Hibbarb et al. 2001) and it is particularly obvious in Africa, Australia and in North and South America (Cabral et al. 2003; Eldridge et al. 2011; Van Auken 2000; D'Odorico et al. 2010; Coetzee et al. 2008).

There is much debate regarding the causes of shrub encroachment. Recently, however, consensus has been emerging on common themes surrounding the causes of shrub encroachment. Encroachment appeared to result from any of a number of distinct factors or interactions of multiple factors that include overgrazing and recovery from anthropogenic disturbance (Scholes and Archer 1997; Coetzee et al. 2008; Van Auken, 2000; Eldridge et al. 2011). The overgrazing hypothesis is based on the premise that sustained heavy grazing reduces above and belowground grass biomass, leading to increased resource availability for the establishment of shrubs, greater shrub recruitment (Coetzee et al. 2008) and therefore reduced fire frequency and intensity (Scholes and Archer 1997; Oba et al. 2000; Roques et al. 2001). With a lack of periodic fires, shrubs and other woody plants have a growth advantage over grasses (Van Auken, 2000). Other causes of shrub encroachment may include increases in CO_2 and N deposition (Scholes and Archer 1997), long-term climate change (Knapp et al. 2008; D'Odorico et al. 2010), the presence of exotic plants and other alterations in local land management practices (Van Auken 2000; Hibbarb et al. 2001; Bond et al. 2003; Knapp et al. 2008).

2.3 Impact of Shrub encroachment

This subsection highlights the impacts of shrub encroachment on soil nutrient properties, plant species diversity and production of the understory vegetation.

Impact of encroachment on soil Nitrogen, Phosphorous and Carbon

Various studies suggest that when the species composition of a community changes due to the spread of woody plants, there is likely to be large impacts on the most important soil nutrients: nitrogen (N) and phosphorus (P), and in the carbon (C) cycling processes (Ehrenfield 2003; Haubensak and Parker 2004; Liao et al. 2008).

Many encroaching species are capable of symbiotic nitrogen fixation (Knapp et al. 2008; Eldridge et al. 2011). Shrubs with N_2-fixing capacity are likely to improve soil nitrogen (Belsky et al. 1989; Liao et al. 2008) and carbon contents (Liao et al. 2008). The mechanism behind the enhanced accumulation of soil carbon in encroached ecosystems is attributed to an increase in above net primary production (ANPP) as a result of increased carbon assimilation via photosynthesis by the encroaching plant species (Liao et al. 2008). The increase in total nitrogen is mainly attributed to N_2-fixation by *Rhizobium* bacteria associated with leguminous shrubs (Sprent, 2009). This results in nitrogen enrichment of the soil through decomposition of root and leaf litter (Baer et al. 2006; Treydte et al. 2007). Brantley and Young (2008) showed that dense thickets of *Morella cerifera* – an N_2-fixing shrub – produced a large quantity of nitrogen–rich litter fall that may rapidly increase both nitrogen and carbon cycling. Furthermore, N_2-fixing plants might have a higher requirement for soil phosphorous (Vitousek et al. 2002), and thus, the spread of N_2-fixing shrubs may induce low levels of phosphorous in the invaded soils (Cech, 2008). The improvement of soil nutrient properties under the canopy of these encroaching shrubs in grasslands gives rise to the term 'islands of fertility' (Treydte et al. 2007). Despite the general improvement of soil nutrient properties, the encroachment of shrubs can lead to negative impacts on plant diversity and plant biomass production depending on the severity of the encroachment.

Impact on understory vegetation composition and production

Shrub encroachment in grasslands is commonly perceived as having a negative effect on biodiversity. The spread of woody plants on floodplain grasslands can be devastating and can potentially alter the basic ecology of grasslands and a range of other effects on the understory vegetation. Rather than adding to the diversity, woody shrubs (especially invasive species) tend to take over creating plant monocultures. Some examples of this includes, *Mimosa pigra* (L.) in Australia (Paynter and Flanagan 2004), Zambia (Shanungu 2009) and Vietnam (Triet et al. 2004). This results in significant negative implications for livestock production and wildlife habitat and nature conservation (Brown and Archer 1999; Ehrenfield 2003; Zedler and Kercher 2004). The changes in plant species diversity and vegetation composition as a result of shrub encroachment are mostly explained by the ability of shrubs to change the microenvironment of the understory. Recent studies suggest that the conversion of grasslands to shrub dominated zones may alter the living conditions of the understory plants through both facilitation and light reduction, thereby causing profound changes in composition and diversity of the vegetation (Pajunen et al. 2011). Reduced light availability is regarded as a major cause of changes in species composition of grasslands accompanying shrub encroachment and has been linked to reduced biodiversity (Kesting 2009). However, this occurs under very high dense stands of shrubs. Contrary to this, Kesting (2009) found that low intensity shrub encroachment could lead to an increase in the actual species richness due to increased habitat heterogeneity brought about by the encroaching shrubs. This is in conformity with the habitat heterogeneity hypothesis in general. According to this hypothesis, shrub encroachment will lead to higher habitat heterogeneity and therefore to higher biodiversity (MacArthur and Wilson 1967).

Studies have shown that in certain areas, small increases in shrub cover can result in drastic reductions in pastoral production because of encroachment (Oba et al. 2000). Thus, shrub encroachment may lead to a reduction in above ground primary production (Hughes, 2006) and the loss of critical wildlife habitat (Adams et al. 1992). The impacts of shrub encroachment are not always negative. Single standing trees of medium to low density usually have a positive effect on understory production, whereas dense woodlands tend to decrease grass cover and productivity due to decreased light intensity (Treydte et al. 2007). Additionally, shrub encroachment could also lead to positive impacts on the understory vegetation. Though many studies focus on the impacts of encroachment on the quantity of herbage, studies on how the shrub encroachment impacts on the quality of the herbage are few (Eldridge et al. 2011). However, these studies indicate that shrub encroachment generally has positive effects on herbage quality (tissue N and P concentrations) due to the 'islands of fertility effect' (Belsky 1992; Treydte et al. 2007; Ludwig et al. 2008). In general, shrub encroachment can lead to drastic reductions in the quantity of herbage but could result in the increase in quality of the understory vegetation. There is a need to understand, therefore, how the loss in the quantity of the herbage can be compensated by the increase in its quality.

2.4 Shrub encroachment on the Kafue Flats

Vegetation change studies on the Kafue flats show that the floodplain grasslands of the Kafue Flats are increasingly being encroached by woody plant species (Munyati 2004; Mumba and Thompson 2005; Genet 2007; Thomas 2007). These studies suggest that the main cause of shrub encroachment on the Kafue Flats is as a result of the changes in the flooding regime brought about by construction of hydroelectric dams both upstream and downstream of the Kafue Flats. Recent investigations about encroachment on the grasslands of the Kafue Flats show linear increase in shrub cover indicating that the encroached areas are expanding and spreading over much of the floodplains of the Kafue flats (Genet 2007; Blaser et al. unpublished). Several reasons have been offered to explain this transformation. The traditional view holds that, after the construction of the Kafue Gorge dam (in 1972) and Itezhi Tezhi storage dam (in 1978) on the Kafue river, the natural cycle of yearly flooding changed and became less dynamic (Genet 2007; Thomas 2007; Gylstra et al. 2008). However, the implication of shrub encroachment on ecosystem properties including soil nitrogen and phosphorous pools and availabilities, soil carbon pools, plant species diversity and herbivory in the Kafue Flats is still poorly known.

2.5 Conclusion

From the body of the reviewed literature, there are no unifying concepts clarifying the impacts of shrub encroachment in grasslands. Impacts of shrub encroachment on various ecosystem functions can either be positive, negative or neutral and this largely depends on the encroaching species in question (Eldridge el al. 2011). Furthermore, the effects of woody encroachment on understory vegetation have mainly been studied under isolated trees or shrubs or in paired open and encroached plots (Belsky 1992; Treydte et al. 2007; Ludwig et al. 2008). However, these studies do not take into account that woody encroachment is a gradual process where understory aspects like productivity, quality and richness of understory vegetation do not necessarily respond linearly to the abundance of the encroaching woody plant (Vetaas 1992; Riginos et al. 2009). Hence there is a need for studies that investigate the characteristics of the understory vegetation along shrub or tree density gradients. This study addressed this gap and showed the impacts of the encroachment of *D. cinerea* and invasive *Mimosa pigra*, an N_2-fixing shrub (Dos Reis et al. 2010), on soil nitrogen (N), phosphorous (P) and carbon (C) pools as well as their impacts on understory plant species diversity and biomass production and on food supply for herbivores along shrub cover gradients.

CHAPTER THREE: DESCRIPTION OF STUDY AREA

3.1 Study Area

The study was conducted in Lochinvar National Park (LNP), Southern Zambia. This section describes in detail, the biophysical characteristics of LNP and in general that of the Kafue Flats Floodplains.

3.1.1 Location

Lochinvar National Park is a small national park occupying an area approximately 410km^2 and located in Southern Zambia between 15^{o}43' and 16^{o}01' South and 27^{o}10' and 27^{o}19' East. It is situated on the southern edge of the Kafue Flats (Figure 1) – a floodplain of the Kafue River, which is a major tributary of the Zambezi River in Zambia.

3.1.2 Climate

The climate in LNP includes three distinct seasons based on temperature and rainfall. The hot and wet season is from November to April, cold and dry season from May to August and then the hot and dry season from September to October. The maximum and minimum temperatures in the flats range from 19 – 36^{o}C in the rainy season and 0 – 21^{o}C in the dry season (Ellenbroek 1987). The average rainfall in Lochinvar averaged 710mm over an eleven-year period from 2000 to 2011. The main period of rainfall is from November up to April and the wettest months are December, January, February and March. Historically, the rainfall over the Kafue Flats is known to be variable on a year-to-year basis and has on several occasions been affected by severe droughts (Ellenbroek 1987).

3.1.3 Flora

The vegetation of LNP is broadly designated into three main vegetation communities: floodplain grasslands, termitara and woodland (Douthwaite 1977; Ellenbroek 1987). These vegetation zones occur in parallel bands as influenced by the altitude above the flood level (Ellenbroek 1987). The floodplain grasslands occur in areas of low elevation between 975m – 981m above sea level and is subjected to prolonged flooding by the water of the Kafue River as well as local runoff and precipitation, the depth of which can reach up to 5m. In the deep waters, the main grasses found are *Oryza longistaminata*, *Vossia cuspidata*, and *Echinocloa stagnina* (Sayer and Van Lavieren 1975). Swampy areas, which remain inundated for most of the year as well as banks of permanent lagoons, channels and oxbows, are covered with *Phragmites mauritianus*, *Cyperus papyrus* and Typha sp (Sayer and Van Lavieren 1975). In the shallow waters, the dominant plant species include *Acrocerus macrum, Leersia denudata*, *Sacciolepis africana* and *Echinochloa pyramidalis* (Ellenbroek 1987; Douthwaite and Van Lavieren 1977). Along the edges of the floodplain, shorter grasses are found such as *Acrocerus macrum* and *Panicum repens* which only tolerate shallow flooding and *Leersia denudata,* which is often mixed with dense stands of the tall sedge *Eleocharis dulcis*. During the last 30 years, the floodplain grasslands of Lochinvar National Park and elsewhere in the Kafue Flats have increasingly been encroached by the exotic and invasive species *M. pigra* (Mumba and Thompson 2005; Thomas 2007; Genet 2007).

The floodplain is bordered by an extensive zone known as termitaria zone comprising of seasonally waterlogged but not flooded grasslands, in which the bush groups are associated with termite mounds (Ellenbroek 1987; Sayer and Van Lavieren 1991). The termitaria zone occurs at elevations of between 981m and 991m above sea level and is charecterised by grasses that include *Acrocerus macrum, Sporobolus ioclados,* *Sporobolus pyramidalis* and *Setaria sphacealata*. Although grasses and woody vegetation on termite mounds characterize this zone, over the last decades, *Acacia sp.,* and *D. cinerea* have been encroaching (Genet 2007).

The woodland zone is confined to the areas that are not flooded and are dominated by three vegetation types, namely, Kalahari woodland, Mopane woodland and munga woodlands (Ellenbroek 1987).

3.1.4 Fauna

Lochinvar National Park is well known for its biodiversity that includes large mammals, amongst them the endemic Kafue Lechwe, Hippo, Sitatunga and small mammals, a diversity of waterbird species, reptiles and amphibians (Douthwaite and Van Lavieren 1977; Ellenbroek 1987). The Kafue Lechwe is a semi-aquatic antelope living on the margin of shallow water and feeds almost entirely on grasses in the water and on dry land. There is an estimated 16,000 Kafue Lechwe in the south bank of the Kafue River the majority of are found in Lochinvar or in the Game Management Area close to the Park (Shanungu and Blaser 2011). At the time of high floods, the Kafue Lechwe are concentrated in the termitaria zone from January to April. As the water recedes in April and May, the Kafue Lechwe begin to move to the floodplain grasslands where they are joined by about 800 Zebra (*Equus burchelli*). Furthermore there are smaller populations of Wildebeest (*Connochaetus taurinus*)*,* Oribi (*Ourebia ourebia*)*,* Impala (*Aepyceros melampus*) and Kudu (*Tragelaphus strepsiceros*) that use the termitaria zone. In the woodland Buffalo (*Syncerus caffer*) and Bushbuck (*Tragelaphus scriptus*) are common.

In LNP, the avifauna is most notable for the diversity and abundance of waterbirds that include palaearctic and intra African rainy season migrants (Douthwaite and Van

Lavieren 1977; Leonard 2005). The species spectrum varies depending on the season and the water level but species which are often found in significant numbers include White Pelican (*Pelecanus onocrotalus*), Common Squacco Heron (*Ardeola ralloides*), Cattle Egret (*Bubulcus ibis*), Openbill Stork (*Anastomus lamelligerus*), Glossy Ibis (*Plegadis falcinellus*), Fulvous Whistling Duck (*Dendrocygna bicolor*), Egyptian Goose (*Alopchen aegyptica*), Spur-winged Goose (*Plectropterus gambensis*), Blacksmith Lapwing (*Vanellus armatus*) and Ruff (*Phylomachus pugnax*) (Leonard 2005).

3.1.5 Geology and Soils

In the woodland zone, ridges of metamorphic Precambrian (Katanga) rock that outcrops locally, run from the south-east to the northwest of Lochinvar giving rise to well drained Loamy soils (Douthwaite and Van Lavierein 1977). The soils are older and poorly drained between the ridges and consist of grey to black alluvial clays. A fault separates the Precambrian rocks of the woodland from the younger Karoo sediments to the north. The Karoo sediments are in turn overlain by recent alluvial deposits of the Kafue Flats (Douthwaite and Van Lavieren 1977). The termitaria zone, which is flat and flooded locally after heavy rains, is overlain by poorly drained deep clay-loams. The clays of the depressions exhibit 'gilgai' microrelief, which is lacking in the sandier clays of the higher ground, adjacent to seasonal streams and ancient drainage channels. The soils of the floodplain are mostly impermeable montmorillonite cracking clays (Douthwaite and Van Lavieren 1977).

3.2 The Study Species

3.2.1 *Dichrostachys cinerea* (L.)

Dichrostachys cinerea (L.) Wight and Arn., is a leguminous shrub belonging to the family of *Fabacea*, subfamily of *Mimosoidea*. It is a semi-deciduous thorny shrub that is capable of reaching 10m tall in its tree stage. *D. cinerea* has a deep taproot and many lateral horizontal roots. It is multi-stemmed with crooked branches hence has an untidy crown (Figure 2). The bi-pinnate feathery leaves, that resemble leaves of *Acacia* sp., have 6 to 19 pairs of pinnae. The spines are unpaired, are similar in colour to the branchlets and reach up to 4cm in length. The inflorescence is a fragrant cylindrical 6 – 8cm long bicoloured spike that bears reddish-purple sterile flowers in the upper part and pale yellow-cream fertile ones in the lower part (Orwa et al. 2009). The seedpods are twisted, indehiscent and are approximately 8cm long (Figure 2). The seedpods are browsed by large mammals (Hagenah et al. 2009) and also can be used as a supplementary feed to livestock (Smith et al. 2005).

D. cinerea is widespread throughout central, southern and tropical Africa and extends up to Asia and Indonesia (Storrs 1995) and is considered to be an important encroacher in African savanna grasslands (Hagenah 2009; Yusuf et al. 2011). *D. cinerea* reproduces by seeds and root suckers. This species is a native invasive woody shrub in savannah grasslands (Yusuf et al. 2011). In Lochinvar National Park, it has encroached on grass-dominated termitaria zone converting a significant proportion of this zone into a woody species community (Genet 2007).

Figure 2: (a) *D. cinerea* shrub in the termitaria zone. (b) Inflorescence of *D. cinerea*. (C) Twisted seedpods of *D. cinerea* in Lochinvar National Park, 2011 (Source: Author, 2011).

3.2.2 *Mimosa pigra* (L.)

Mimosa pigra (L.) is a leguminous shrub that belongs to the family *Fabaceae* and subfamily *Mimosoideae*. A native to tropical America, *M. pigra* is now widespread throughout the world's tropical and subtropical wetlands (Lonsdale et al. 1989). *M. pigra* is a spiny terrestrial shrub that grows up to 2 – 6 meters in height and forms thick impenetrable monospecific stands (Figure 3). Leaves are bipinnate, consisting of a central prickly rachis 20 to 25cm long with up to 16 pairs of pinnae which are 5cm long, each divided into pairs of leaflets (Miller and Pickering 2001). Flower heads are round fluffy balls consisting of up to 100 small pink to mauve coloured flowers (Figure 3). Seedpods are segmented and turn brown when mature (Miller and Pickering 2001). *M. pigra* grows in moist sites such as floodplains, coastal plains and along river banks (Paynter 2004). Since the early 1980s, *M. pigra* has invaded the Kafue Flats, especially within the floodplains of Lochinvar National park (Mumba and Thompson 2005; Thomas 2007). *M. pigra* started with a small infestation of about 2 ha in the early 1980s and quickly spread to at least 1950ha by 2005 (Genet 2007). It now occupies a significant proportion of the floodplains of Lochinvar National park and is still spreading (Shanungu 2009). *M. pigra* is a very invasive (Buckley et al. 2004; Paynter & Flanagan 2004). It displaces native vegetation and animals from large areas of land, seriously affecting conservation, tourism and traditional use of wetlands by local people (Kampamba and Nyirenda 2004).

Figure 3: (a) *M. pigra* shrubs along the banks of the Nampongwe stream in LNP. (b): Seedpods and flower of *M. pigra*. (c): Dense *M. pigra* stand in Lochinvar National Park, 2011. (Source: Author 2011).

CHAPTER FOUR: METHODOLOGY

4.1 Study Design and Study Site Selection

Shrub encroachment on the Kafue Flats has resulted in landscapes of a mosaic of *D. cinerea* and *M. pigra* with varying degrees of densities (Genet 2007; Thomas 2007; Blaser et al. unpublished). Based on a series of field surveys, aerial photographs as well as vegetation maps (Turner 1985), and aerial reconnaissance surveys (in February 2008), information about the spatial distribution of *M. pigra* and *D. cinerea* in Lochinvar National Park was obtained. In general, *M. pigra* mainly encroaches in the floodplain grasslands whereas *D. cinerea* encroaches in the termitaria vegetation zone. Therefore, even though these two shrub species are encroaching at the same time, they occupy different ecological niches.

The overall objective of this study was to determine how ecosystem properties change with increasing canopy cover of *D. cinerea* and *M. pigra*. In this regard, selection of the plots was done so as to represent a wide range of shrub encroachment from nearly shrub-free grasslands to sites with very dense shrub cover. This approach to determining changes in ecosystem properties accompanying shrub encroachment has been used in other studies in Southern Africa (Blaum et al. 2009; Sirami et al. 2009) and elsewhere (Hughes et al. 2006)

Along the *D. cinerea* gradient of increasing shrub cover, twenty (20) 10m x 10m plots were established (Figure 4) in Lochinvar National Park. The plots ranged from 0% to 100% cover of *D. cinerea.* This was done in order to determine if there was a direct relationship between the soil and plant variables with increase in the cover of *D.*

cinerea. The plots were then aggregated by ascending shrub cover into four shrub classes each containing five plots.

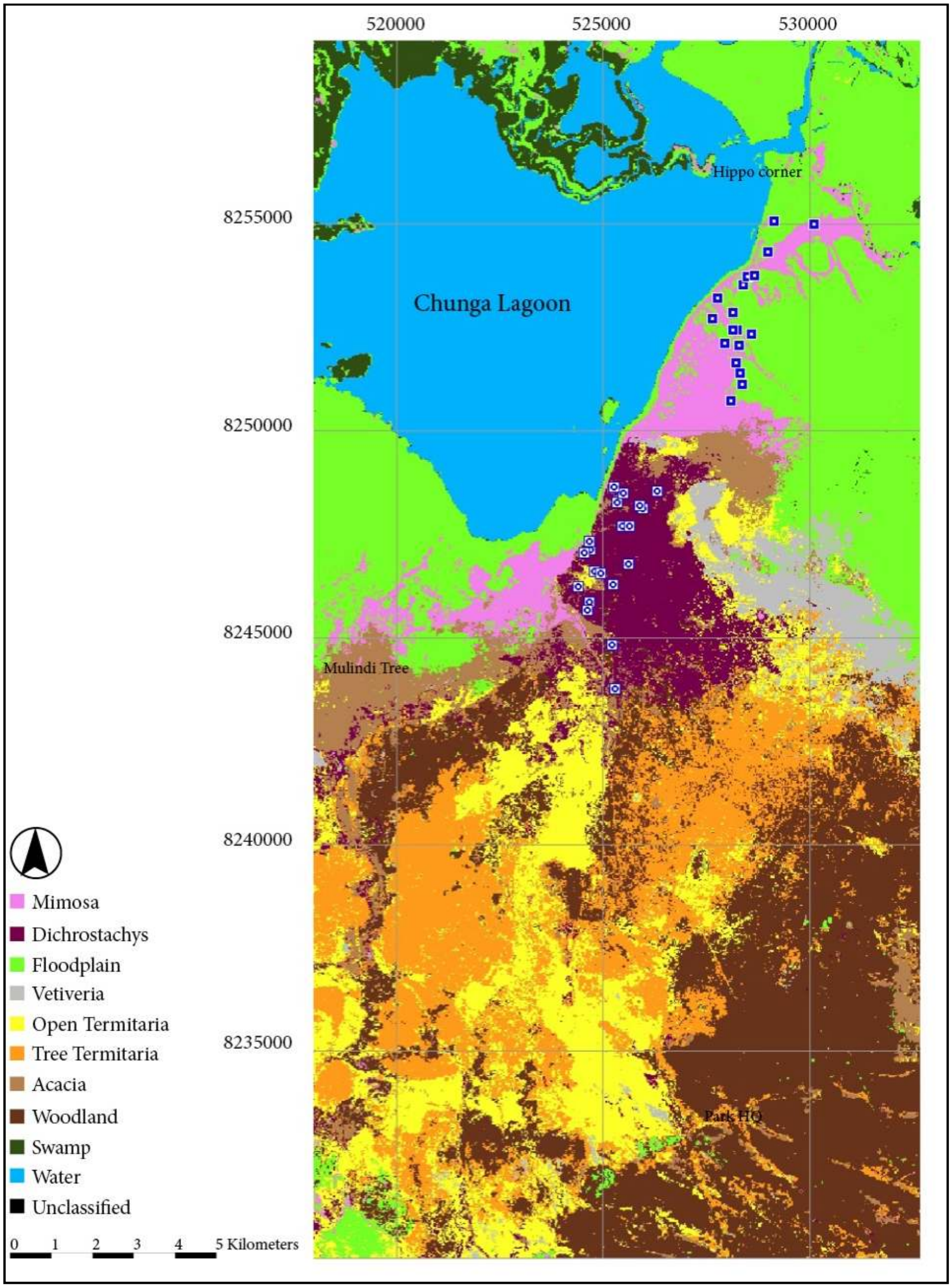

Figure 4. Location of sampling plots in the *D. cinerea* (purple) and *M. pigra* (pink) encroached sites. (Source: Author 2012)

The four shrub classes ranged from low encroached grasslands (0 to 20% shrub cover), moderately encroached (25 to 40% shrub cover) and densely encroached (50 to 70% shrub cover) and very dense sites (75 to 95% shrub cover). Figure 5 shows a pictorial illustration of the different shrub classes along the *D. cinerea* gradient. In the *M. pigra* gradient of increasing shrub cover, a total of eighteen (18) plots (10m x 10m in size) were established. The plots were then aggregated by ascending shrub cover into three shrub classes each containing six plots. The three shrub classes ranged from low encroached grasslands (5 to 40% shrub cover), moderately encroached (45 to 60% shrub cover) and densely encroached (65 to 100% shrub cover).

The latitude and longitudes were recorded for each plot using a Global Positioning System (GPS).

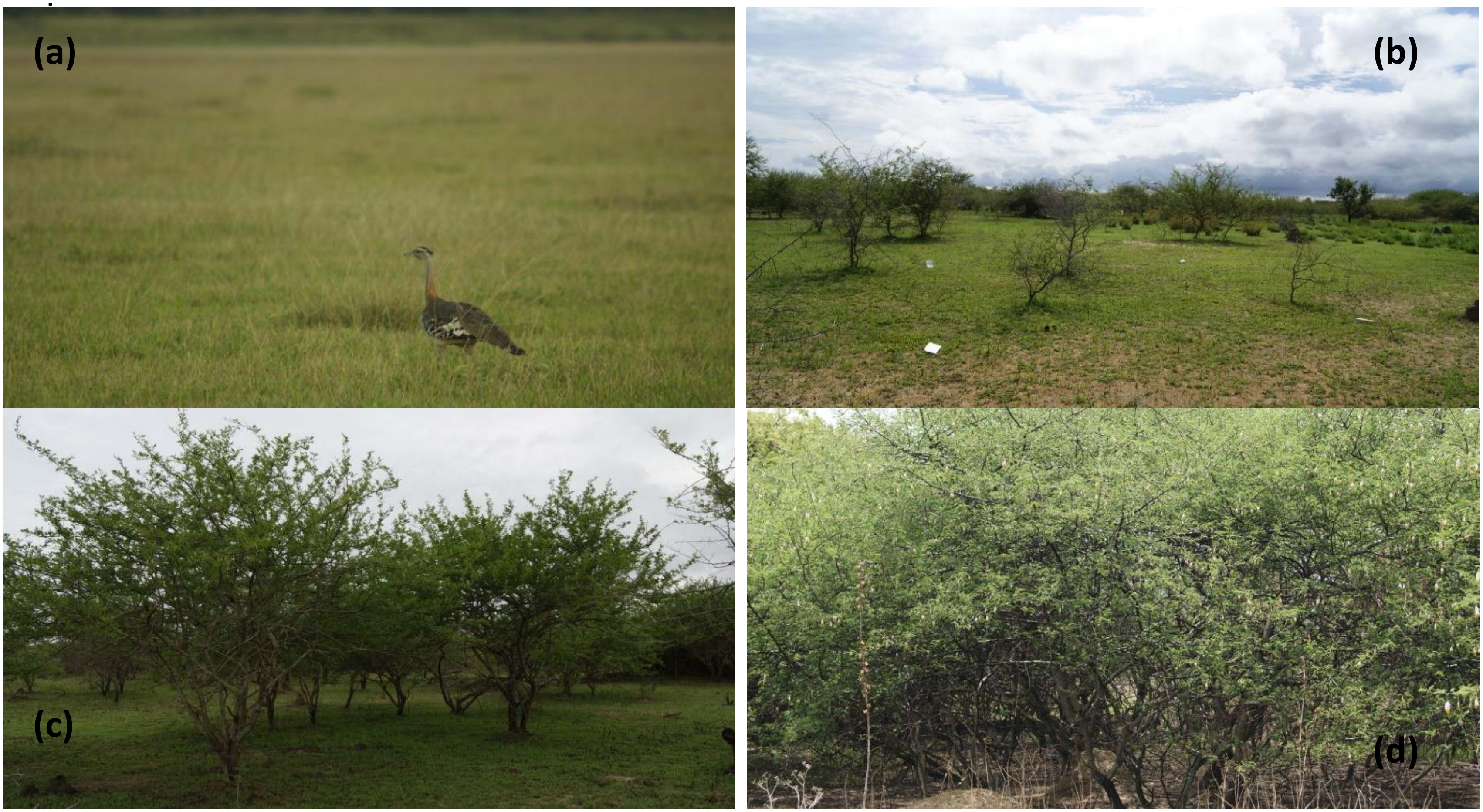

Figure 5. (a) Open termitaria grassland with no shrub encroachment (b) lowly encroached termitaria grassland (c) moderately encroached termitaria grassland and (d) densely encroached termitaria grassland in Lochinvar National Park, 2011. (Source: Author 2011).

4.2 Data Collection

4.2.1 Impact of Shrub Encroachment on Soil PH, Bulk Density, Soil Moisture, Soil Nutrient Pools and Availabilities and Light.

To determine if shrub encroachment alters soil properties, soil samples were collected along the gradient of increasing shrub cover of *D. cinerea* and *M. pigra* and analysed for (i) Bulk density (ii) nitrogen, phosphorous and carbon concentration, (iii) nitrogen mineralisation rate, (iv) soil pH and (v) nitrogen and phosphorous availabilities. In addition, light measurements were conducted along the gradient of *D. cinerea*. Methods to determine these parameters are described in the following sections below:

a) Determining the relationship between shrub encroachment and soil nutrients.

Soil samples were taken from all sampling plots in the *D. cinerea* and *M. pigra* gradients of increasing shrub cover during the early growing season (December 2010) and repeated in the mid growing season (February 2011) but only limited to the *D. cinerea* gradient. Three soil cores were used to collect soil samples from each plot. All the soil cores used were 5cm in diameter and 15cm long. Each soil core was placed 2 meters diagonally from the middle of the plot towards three of the four corners of the plot. After removal of standing litter, soil samples were collected from the upper 10cm of the soil. Soils from all the three cores were then pooled in a bag and mixed thoroughly. Pooled soil samples were dried in a solar drying oven until constant weight. Soil bulk density (in g/cm^3) was determined by dividing the dry weight of soil samples by the volume of the sample. After that, roots and larger pieces of wood or stones were removed and the samples were ground and passed through a 0.5mm sieve. A subsample of the ground soil was collected and transported to ETH – Zurich for analysis of total nitrogen, phosphorous and carbon concentrations. Nitrogen and phosphorous concentrations were measured colorimetrically after Kjeldahl digestion (Allen 1989), using an auto analyzer (Seal, Analytical). Total organic carbon and nitrogen were determined using a dry combustion analyzer (CN-2000, LECO Corp., St Joseph, Minesota USA). The soil nitrogen, phosphorous and carbon concentrations were expressed as mg/g of soil.

b) Determining the relationship between shrub encroachment and Nitrogen mineralization rates and inorganic Phosphorous pools.

Mineralization of nitrogen can be determined by measuring inorganic nitrogen at the start and the end of an incubation period. By subtracting the initial amounts of nitrogen from the final amounts, the mineralization rate can be calculated (Verhoeven et al. 1990). To measure nitrogen mineralization rates and the inorganic phosphorous pools of the soil in this study, three pairs of soil cores were collected in each plot of the *D. cinerea* gradient. All the soil cores were collected 2m from the center of the plot from the upper 10cm of the soil. One of each pair of soil cores was put in a bag and transported to the field laboratory in Lochinvar for analysis. In the field laboratory, pooled soil cores were manually sorted, roots were removed, and soil extractable nitrogen and phosphorous pools were determined. The other pair was incubated by covering both ends of the soil core with plastic lids and incubated ex-situ in a representative termitaria plot in order to measure the accumulation of extractable nitrogen in the subsequent incubation period. *In situ* incubations were not possible because of the risk of flooding in some sites. The soil cores were incubated for four weeks and after incubation, the soil core from each site was removed from the soil cores and pooled and transported to the Laboratory in LNP for nitrogen and phosphorous extractions.

The soil extractable nitrogen pool was determined by extraction of 5g fresh soil in 50ml 0.2M KCl for one hour. The extractable phosphorous pool was determined as extractable PO_4^{2-} by extraction of 5g fresh soil with 50ml Bray-II extraction solution (Bray and Kurtz, 1945). All extractions were done within 12h of collection of the soil cores and stored frozen until further analysis. The extracted samples were transported to ETH-Zurich where they were analyzed for NH_4^+, NO_3^- and PO_4^{2-} concentrations calorimetrically using a flow injection analyzer (Seal Auto Analyzer 3, XY – 2 Sampler, Seal Analytical, Australia). The net nitrogen mineralization rate was calculated as the difference between the extractable nitrogen at the start and at the end of the incubation period divided by the number of days of the incubation (Olff et al. 1994). Soil pH was also measured from the KCL extract.

Due to extensive flooding during the sample collection period, it was not possible to collect soil samples from 3 plots in the *Mimosa pigra* gradient.

c) Determining the relationship between shrub encroachment and soil nutrient availability.

To determine the plant available phosphate, ammonium, nitrite and nitrate in the soil, the Ion Exchange to Resin (IER) bag method was used (Binkley and Matson 1983). IER bags were prepared by placing 2g of mixed-bed ion-exchange resin (Amberlite IRN 150, H^+- and OH^--form, Sigma-Aldrich, Switzerland), in 5x5cm bags made of fine nylon fabric (60 µM mesh width, Sefar Nitex 03- 60/35, Sefar AG, Thal, Switzerland). The IER bags were then saturated with K^+ and Cl^- ions by shaking them for two hours in 2M KCl solution. After shaking, the IER bags were rinsed thoroughly with distilled water. The resin bags were then stored at 4°C in an airtight zip bag until use. Four IER bags were placed diagonally in each plot 2m from the center of the plot.

Each bag was placed carefully in the soil at 5cm depth in a 45 degrees slant incision made with a knife after which the slant was closed. The resin bags were removed from the soil after 30 days, cleaned with distilled water, air dried and transported to ETH – Zurich for analysis. At ETH-Zurich, the IER bags were extracted in 30ml of 1M KCl by shaking for one hour. Then the extracts were diluted to 0.2M and analyzed in a flow injection analyzer (Seal Auto Analyzer 3, XY – 2 Sampler, Seal)

d) Determining the relationship between shrub encroachment and light reaching the understory vegetation.

Light was measured in each plot along the *D. cinerea* gradient in May 2011. In each plot, light was measured at 9 points as illustrated in Figure 6 below. At each point a light sensor (Photosynthetically Active Radiation (P.A.R) Sensor - JYP 1000) was placed at 4 layers – 0cm, 20cm, 60cm and 1m above ground – and the light intensity was measured and recorded.

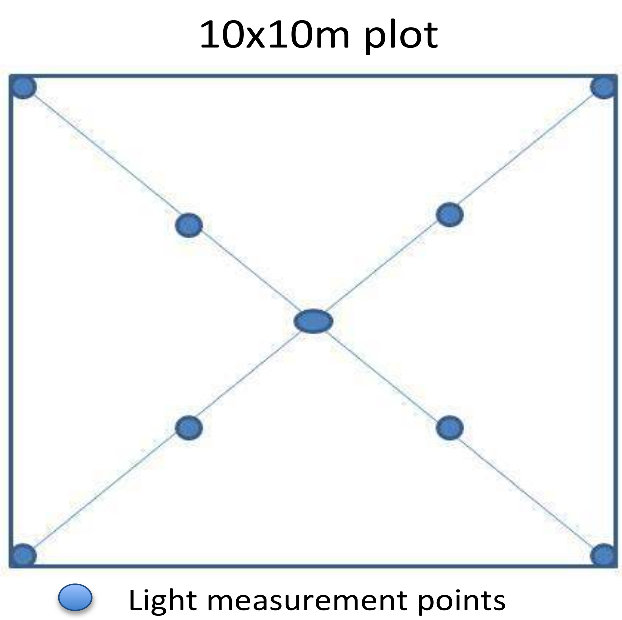

Figure 6. Illustration of the Light measurements points in the 10x10m plot along the *D. cinerea* gradient.

As a reference, light was measured in an open site adjacent to each plot. The amount of light in each plot on all the different layers was calculated as a percentage of the amount of light in the open reference using the formula below:

Amount of light in plot = light measured in plot/light in reference plot * 100

The mount of light was averaged at each layer from all the nine points of measurement. Light measurements were carried out between 11 and 13hours, when the sun was overhead, and care was taken to measure light during cloudless times.

4.2.2 Impact of Shrub Encroachment on Plant Species Diversity and Vegetation Composition.

In order to assess the impacts of shrub encroachment on plant species diversity and changes in vegetation composition along the gradient of increasing cover of *D. cinerea* and *M. pigra*, vegetation recordings for all the plots in these gradients were conducted. Species composition of the vegetation was recorded in each plot in April and May 2010 using the vegetation releveé method (Mueller-Dombois and Ellenberg 1974, MDNR 2007). Within each plot the occurrence of all vascular plants was listed as presence-absence data (Appendix 1) and their percentage cover, as a measure of abundance, was estimated visually using the Braun-Blanquet cover class scale (Mueller-Dombois and Ellenberg 1974). The percent cover of each species was assessed as the vertical projection onto the ground of all the above ground parts of the species expressed as a percentage of the reference area. Unidentified plants in each plot were collected following standard herbarium techniques for later identification. Identification of the herbaceous species was conducted at the Lochinvar National Park Herbarium and through consultations with experts. Nomenclature of the plant species followed Flora Zambeziaca and Ellenbroek (1987).

Plant species richness and diversity

To quantify the diversity of the plant species in each plot, the Shannon-Wiener Diversity index (H') as a measure of species abundance and richness was applied. This index which takes both species abundance and species richness into account is sensitive to changes in the importance of the rarest classes and is the most commonly used index (Kent and Coker 1992). The Shannon-Wiener Diversity Index, H', was calculated using the statistical package PC-ORD 5.10 (McCune and Mefford 2006), by using the equation:

$$H' = -\sum P_i (\ln P_i)$$

where P_i is the proportion of the cover of each species in the plot (Whittaker 1972). Species richness was estimated as the total number of species inventoried in the plot.

4.2.3 Impact of Shrub Encroachment on the Food Supply for Herbivores.

In order to determine if shrub encroachment reduces the food supply for herbivores, parameters such as grass cover and forb cover, total standing biomass, herbage production, total grass biomass and grass biomass production were measured in the plots along the *D. cinerea* and *M. pigra* gradients. Additionally, the quality of the herbage in the *D. cinerea* and *M. pigra* gradients was determined.

To measure the Total standing biomass and herbage production of the herbaceous vegetation, the movable cage method was used (McNaughton et al. 1996). In each gradient, 10 representative plots distributed evenly within each shrub cover class were selected. At time one (t=1), in December 2010, one moveable cage ($1m^2$) was placed in each plot and two reference plot ($1m^2$) with the same vegetation and ground cover were selected. The movable cage was used so as to prevent grazing of the vegetation in the plot by Lechwe and other ungulates. Biomass was clipped to ground level in a 50cm x 50cm ($0.25m^2$) quadrat in the center of one reference plot. The cut biomass was separated into dry and fresh biomass. The dry biomass was discarded and the fresh biomass was further separated into functional groups i.e. grasses and forbs and dried using a solar drying oven for three weeks at 50^oC and weighed (g/m^2). The combined mass of grasses and forbs was taken as the initial biomass for the plot.

After six weeks (t=2) the biomass in the movable cages as well as in the unclipped reference plots was cut in a 50cm x 50cm ($0.25m^2$) quadrat. A new reference and a cage location with the same vegetation and ground cover as the unclipped reference were chosen for the subsequent period. The biomass was then separated into functional groups as well as dead and alive plant material, dried and weighed. The difference in the initial biomass in the reference plot (t=1) and the biomass in the cage (t=2) was calculated and this was taken as the biomass production of the plot. Total standing biomass and herbage production for the entire $100m^2$ was calculated by scaling up from the 0.25 m^2 plots (assuming homogenous conditions in the site).

In the dense *M. pigra* plots, it was not possible to place the cages evenly as the *M. pigra* forms thick impenetrable thickets. And so the cages were placed in the open spaces between the thick shrubs and the biomass was measured in the open spaces between the shrubs. Afterwards, the biomass for the entire plot $100m^2$ with *M. pigra* encroachment was quantified. To quantify the biomass for the whole $100m^2$, the formula indicated below was used:

Biomass in $100m^2$ plot with *M. pigra* = X (100% - Y%) /100%

Where: X = biomass in $100m^2$ plot assuming no *M. pigra* encroachment

Y = Percentage cover of *M. pigra* in the 100m^2 Plot.

This approach assumes that where *M. pigra* grows, all other forms of vegetation do not grow. In the field, most of the areas where the *M. pigra* was growing did indeed not have any other plants growing under it especially in the very dense sites. The calculated biomass is not extremely accurate but is a good estimate of the quantity of biomass taken away by the encroachment of *M. pigra.*

4.2.4 Impact of shrub encroachment on Herbage quality

A subsample of the grass biomass harvested from each site (reference plot) was collected and transported to ETH – Zurich where the quality of the grass was determined. Quality in this study is defined as the nitrogen and phosphorous concentrations in the grass biomass, which are essential macronutrients for herbivores (Treydte et al. 2007). The concentration of nitrogen and phosphorous in the grass biomass was measured colorimetrically after Kjeldahl digestion using an auto analyzer (Seal, Analytical). Additionally, the vegetation N:P ratio was computed to predict the nature of nutrient limitation in the ecosystem (Koerselman and Meuleman 1996).

4.3 Data Analyses

4.3.1 Impact of Shrub Encroachment on Soil Characteristics

Differences in Nitrogen, Phosphorous and Carbon concentrations among different shrub cover classes.

One-way Analysis of Variance (ANOVA) was used to test for differences in soil nitrogen, phosphorous and carbon among the shrub cover classes in the *D. cinerea* and *M. pigra* gradient. When differences were found among the shrub cover classes, a Newman-Keuls multiple comparison test was used to perform pairwise comparisons to determine which cover classes the differences existed. Statistical decisions were made at p=0.05 unless otherwise stated.

A t-test assuming unequal variances was performed to determine if there were differences in the amount of nitrogen, phosphorous and carbon in the soils from the *D. cinerea* and *M. pigra* encroached plots. Statistical decisions were made at p=0.05 unless otherwise stated. ANOVA and t-test were performed using WINKS SDA Software (Texasoft 2007).

Relationship between increasing shrub cover and soil characteristics.

Effects of shrub encroachment on soil nutrient properties were analyzed by linear and quadratic regression models. First, a linear regression was performed with the soil characteristics (nitrogen, phosphorous and carbon concentrations, nitrogen mineralization rate and nutrient availabilities, soil bulk density, pH and moisture) of the plots taken as the dependent variables and the cover of the shrubs as the independent variable. The regression analysis was then repeated by adding the quadratic fit. To determine the significance of regression ANOVA of the independent variable on the dependent variable was carried out. The probability significance of

0.05 was used. Models were developed for the relationship between shrub cover and soil characteristics and summarized in the equation of a straight line and quadratic equation as appropriate. The quadratic fit was favoured over the linear fit if the quadratic fit had a lower *P* value and higher R^2 than that of the linear fit. Statistics were performed using the statistical program JMP Version 5.0.1.2 (SAS 2006).

4.3.2 Impact of Shrub Encroachment on Plant Species Diversity and Vegetation Composition.

In order to examine the impact of increasing cover of shrubs on plant species diversity, regression analysis was applied. First, linear models were applied and the R^2 values noted. Then a quadratic term was added in order to check if it significantly added to the overall model.

Further, Detrended Correspondence Analysis (DCA) ordination technique was used to study the distribution of plant species along the *Dichrostachy cinerea* and *Mimosa pigra* gradients. Detrended correspondence analysis (Hill and Gauch 1980) is an Eigen analysis ordination technique based on reciprocal averaging. The DCA performed included all individual species in the plot and the analysis used the Braun-Blanquet cover estimates for each species from each plot as the abundance measure. For detrending, a default value of "26" recommended by ter Braak (1987) was used. Rare species were down weighted in the DCA ordination. Ordinations were performed on the sample plots using the statistical package PC-ORD 5.10 (McCune and Mefford 2006).

4.3.3 Impact of Shrub Encroachment on the Food Supply for Herbivores.

Relationships between increasing shrub cover and total standing biomass, herbage production and total grass biomass and grass biomass production were analysed using linear and quadratic regression models. First, a linear regression was performed with the total standing biomass, herbage production, grass biomass and grass biomass production taken as the independent variables and the shrub cover taken as the dependent variable. The regression analysis was then repeated by adding the quadratic fit. To determine the significance of regression, ANOVA of the independent variable on the dependent variable was performed. The probability significance of 0.05 was used. Models were developed of the relationship between shrub cover and soil characteristics and summarized in the equation of a straight line and quadratic equation. The quadratic fit was favoured over the linear fit if the quadratic fit had a lower *P* value and higher R^2 than that of the linear fit. Statistics were performed using the statistical program JMP Version 5.0.1.2 (SAS 2006).

CHAPTER FIVE: RESULTS

5.1 Impacts of Shrub Encroachment on Soil Nutrient Pools, Availabilities and Other Micro-Environmental Conditions

Differences in Nitrogen, Phosphorous and Carbon Concentrations among Different Shrub Cover Classes.

In the *D. cinerea* plots, soil nitrogen ranged from 0.29mg/g to 1.501mg/g, soil phosphorous concentration ranged from 0.0067mg/g to 0.253mg/g and soil carbon concentration ranged from 4.59mg/g to 15.01mg/g. In the *M. pigra* plots, the soil nitrogen concentration ranged from 2.24mg/g to 4.33mg/g and soil phosphorous concentration from 0.0165mg/g to 0.2048mg/g. Soil carbon ranged from 25.64mg/g to 49.51mg/g in the *M. pigra* plots. Data for the mean concentration of nitrogen, phosphorous and carbon in the shrub cover classes for *D. cinerea* as well as ANOVA results are summarized in Table 1. Results from the ANOVA indicates that there were marginally significant differences in the mean nitrogen concentration across the shrub cover classes $F (3, 15) = 3.27$, $p = 0.05$. The mean nitrogen concentration increased from 0.633mg/g in the low shrub cover class to 0.922mg/g in the very dense shrub cover class. No significant differences existed in the mean phosphorus concentrations, $F (3, 15) = 1.78$, $p = 0.19$ between the shrub cover classes. However, significant differences were found across the shrub cover classes for carbon concentration in the soil $F (3, 16) = 8.13$, $p = 0.0016$. A Newman-Keuls multiple comparison procedure was performed at the alpha=0.05 significance level to determine specific pairwise differences in the carbon concentration. This test indicated that significant differences in mean carbon concentration existed between very dense and all other shrub classes. Similarly, differences existed between low and medium shrub cover classes whereas no significant differences existed between medium and dense shrub cover classes. Additionally, the mean carbon concentration was highest in the very dense shrub cover class and lowest in the low shrub cover class indicating an increase in carbon concentration from low to very dense shrub cover (Table 1).

Table 1: Mean concentration ± standard deviation of Nitrogen, Phosphorous and Carbon in the shrub cover classes of *D. Cinerea* as well as one-way ANOVA results to compare means among the shrub cover classes (Source: Field data, 2011).

	Dichrostachys cinerea							
	Cover classes				ANOVA			
	Low	Medium	Dense	Very dense	df	MS	Fvalue	P value
Nitrogen	0.633±0.147	0.67±0.13	0.731±0.035	0.922±0.235	(3,15)	0.08	3.27	0.0508
Phosphorous	0.048±0.016	0.065±0.029	0.049±0.023	0.099±0.066	(3,15)		1.78	0.1944
Carbon	6.537±2.033	8.579±1.602	8.275±1.827	12.212±1.984	(3,16)	3.49	8.13	0.0016

Data for the mean concentration of nitrogen, phosphorous and carbon in the shrub cover classes for *M. pigra* as well as ANOVA results are summarized in Table 2. ANOVA results indicate that no differences existed in mean concentration of nitrogen, phosphorous and carbon among the cover classes.

Table 2 Mean concentration ± standard deviation of nitrogen, phosphorous and carbon in the shrub cover classes of *M. pigra* as well as one-way ANOVA results to compare means among the shrub cover classes. (Source: Field Data, 2011).

	Mimosa pigra						
	Cover classes			**ANOVA**			
	Low	Medium	Dense	df	MS	Fvalue	Pvalue
Nitrogen	3.143±0.69	3.833±0.408	3.5±0.707	(2,12)	0.35	2.21	0.153
Phosphorous	0.127±0.046	0.108±0.065	0.112±0.091	(2,12)	0.0035	0.181	0.837
Carbon	38.0±5.89	43.50±4.76	40.895±0.205	(2,12)	26.79	1.83	0.202

Comparison of mean concentration of nitrogen, phosphorous and carbon between D. cinerea and M. pigra plots

Across the *D. cinerea* plots, the mean concentration of nitrogen (0.721mg/g) was significantly lower ($t= -19.15$, $p < 0.05$) compared to the mean concentration of nitrogen (3.516 mg/g) in the *M. pigra* plots. The same was observed for the mean concentration of Carbon (8.809mg/g) in *D. cinerea* compared to mean concentration (40.854mg/g) in the *M. pigra* plots ($t= -19.81$, $p<0.05$). The mean phosphorous concentration was also lower in the *D. cinerea* plots (0.063mg/g) compared to the mean concentration in the *M. pigra* plots (0.117mg/g) ($t= -2.44$, $p<0.05$). Overall soil nitrogen, phosphorous and carbon pools were approximately 5-10 times higher in the *M. pigra* gradient than in the *D. cinerea* gradient.

Relationship between increasing shrub cover and soil characteristics.

There was a positive correlation between the concentration of soil carbon ($r^2=0.45$, $p<0.005$), nitrogen ($r^2=0.47$, $p<0.005$) and phosphorous ($r^2=0.24$, $p<0.03$) with shrub cover along the *D. cinerea* gradient. As shrub cover of *D. cinerea* increase, the concentration of soil carbon, nitrogen, and phosphorous increased significantly (Figure. 7A, 7 C and 7E). In the *M. pigra* gradient soil carbon ($r^2=0.1$ $p=0.25$), nitrogen ($r^2=0.07$, $p=0.25$) and phosphorous pools ($r^2=0.01$, $p=0.79$) were not correlated to shrub cover (Figure. 7B, 7D and 7F).

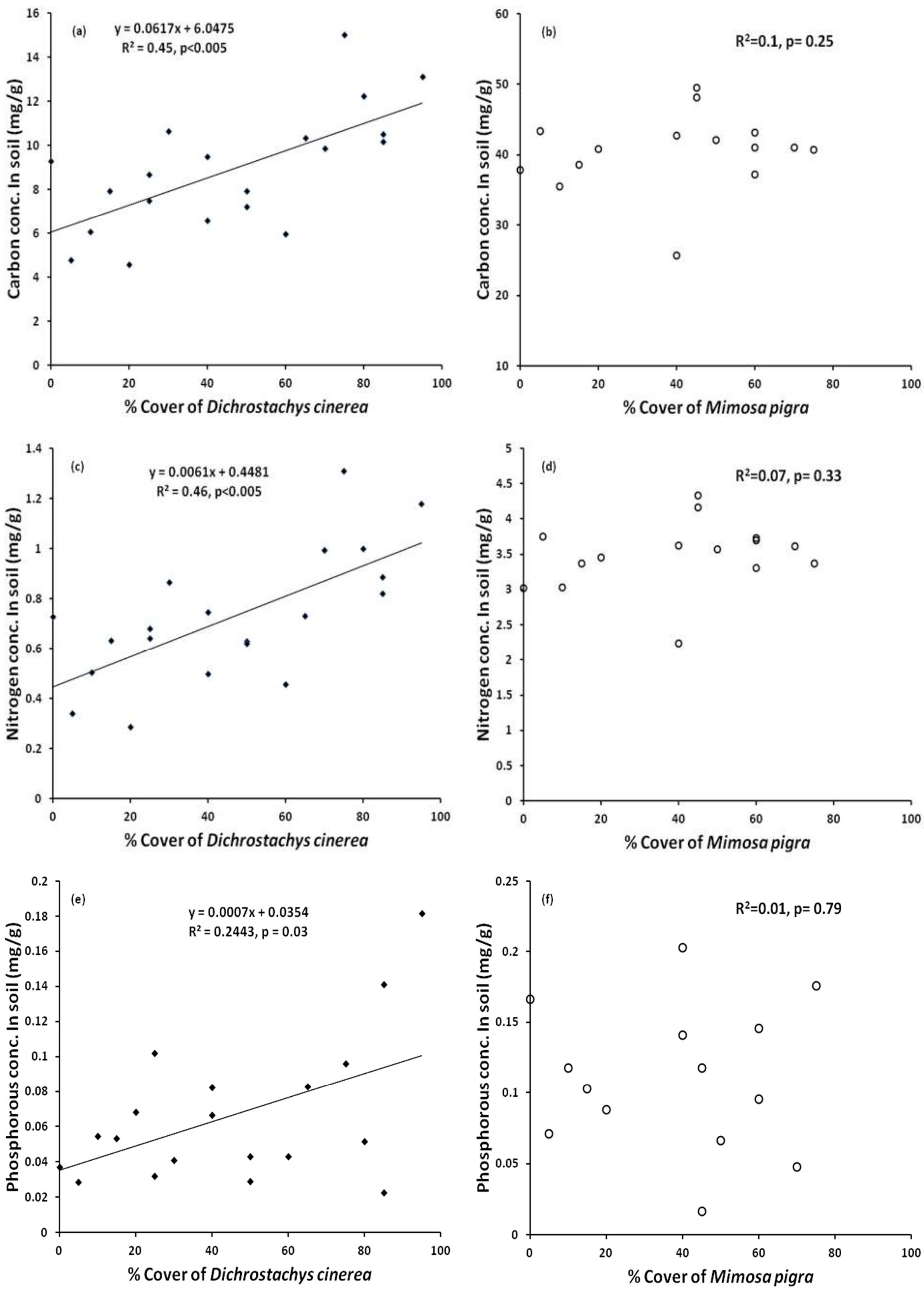

Figure 7: Total C, N and P soil pools (at 10cm soil depth) along cover gradients of *D. cinerea* (A, C, E) and *M. pigra* (B, D, F) gradients, December 2010. Note that the Y-axis differs among the panels. (Source: Field data, 2011).

Results of correlation and regression analysis between shrub cover of *D. cinerea* and *M. pigra* with soil characteristics are summarized in table 3. The analysis showed that nitrogen adsorption to resin (or nitrogen availability) increased with increasing cover of *D. cinerea*, but soil extractable N and N mineralization rate were not correlated to cover of *D. Cinerea* (Table 3). Soil extractable phosphorous increased with increasing cover, but phosphorous adsorption to resin (or phosphorous availability) was not correlated to the cover of *D. Cinerea* (Table 3). In the *M. pigra* gradient, adsorbed nitrogen and phosphorous to resin (nitrogen and phosphorous availabilities) were not correlated with increasing cover of *M. pigra* (Table 3). Similarly, Bulk density, pH and soil moisture of the soil was not correlated with increasing cover of shrubs in both the *D. cinerea* and *M. pigra* gradients (Table 3).

Table 3: Results of linear regression analysis of increasing shrub cover with a range of soil variables; the statistics given are mean values of the variables followed by standard deviation, square of correlation coefficient and the significance of the regression ANOVA indicated as p. (Source: Field data, 2011).

	Dichrostachys cinerea			**Mimosa pigra**		
	Absolute value (mean ± std)	R^2	p	Absolute value (mean± std)	R^2	p
Environmental variables						
Bulk density (g cm^{-3})	11.71 ± 1.17	0.06	0.29	5.83 ± 1.27	0.26	0.05
Soil pH	4.64 ± 0.48	0.05	0.36	4.55 ± 0.23	0.001	0.91
Soil moisture (%)	11.17 ± 4.1	0.02	0.55	31.9 ± 13.08	0.06	0.39
Extractable P (mg/g soil)	0.004 ± 0.003	0.27	0.02	-	-	-
Extractable N (mg/g soil)	0.008 ± 0.002	0.02	0.54	-	-	-
N mineralization (mg/g/d)	0.0002±0.0002	0.01	0.66	-	-	-
Absorbable P (mg/g resin) (Dec, 10)	0.0001±0.0005	0.09	0.19	0.00001±0.000005	0.0005	0.94
Adsorbable N (mg/g resin) (Dec, 10)	0.003 ± 0.003	0.3	0.01	0.0092±0.01	0.0002	0.97
Absorbable P (mg/g resin) (Feb, 11)	0.0002±0.0004	0.05	0.33	-	-	-
Adsorbable N (mg/g resin) (Feb, 11)	0.005 ± 0.004	0.29	0.02	-	-	-

Light

Light decreased with increasing cover of the *D. cinerea* shrub at both the soil surface and 1meter above ground (Figures 8A and 8B).

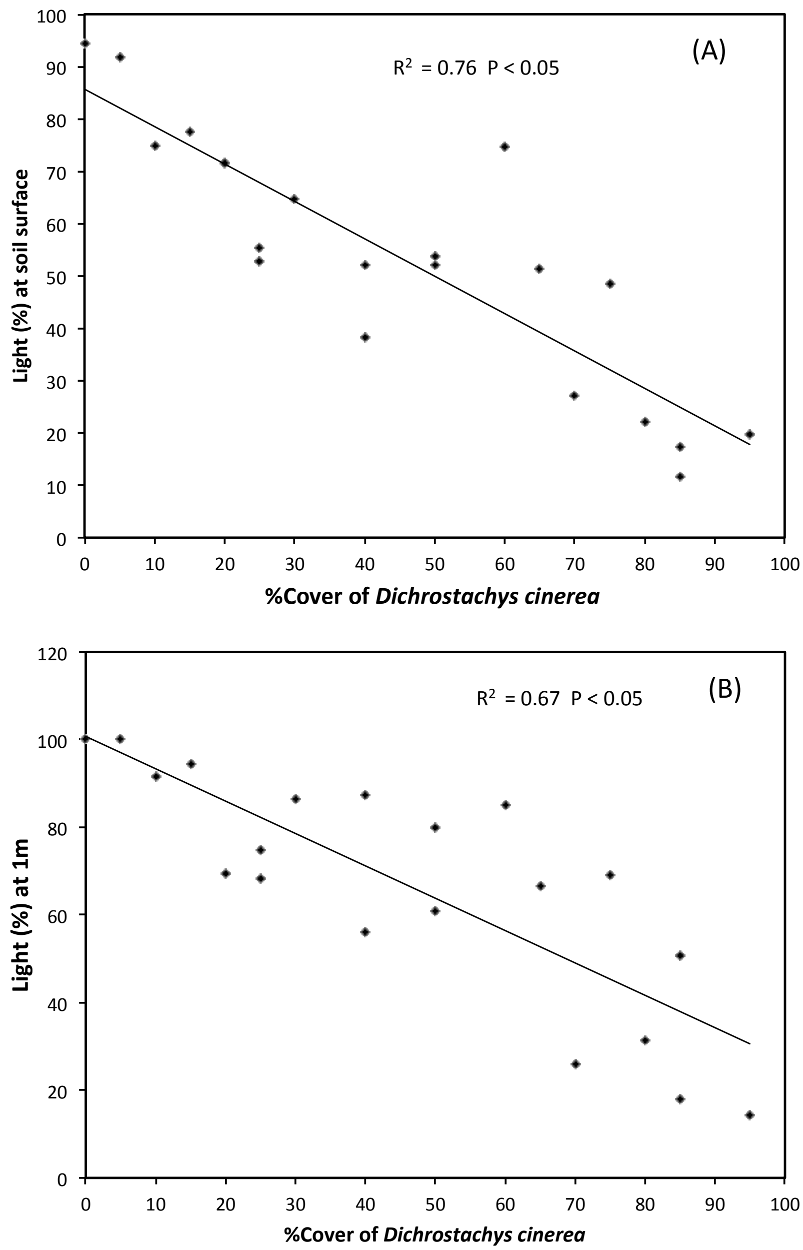

Figure 8: Relationship between shrub cover and light (%) on understory vegetation at soil surface (A) and one meter above the soil surface (B).(Source: Field data, 2011)

5.2 Impact of Shrub Encroachment on Vegetation Composition and Species Richness and Diversity.

Impact of increasing cover of D. cinerea on plant species richness and diversity

A total of 84 plant species were recorded along the *D. cinerea* gradient, 28 grasses and 56 forbs (Appendix 2). Species richness (total number of plant species per 10x10 m plot) ranged from 11 to 31, and showed a marginally significant quadratic relationship (or hump-backed) with *D. cinerea* cover ($r^2 = 0.291$, $p = 0.053$). Plant species diversity (H') showed a similar but significant quadratic relationship with *D. cinerea* cover, ($r^2 = 0.318$, $P = 0.02$) (Figure 9). Maximum species richness and diversity (H') was reached at about 40% shrub cover, and species richness and diversity in the densest shrub lands was throughout lower than in the open grasslands (Figure 9). With an increase in shrub cover (particularly above 80%) the number of grass species significantly declined ($r^2 = 0.53$, $p<0.05$), but the number of forb species was not affected by shrub cover ($r^2=0.09$, $p=0.21$).

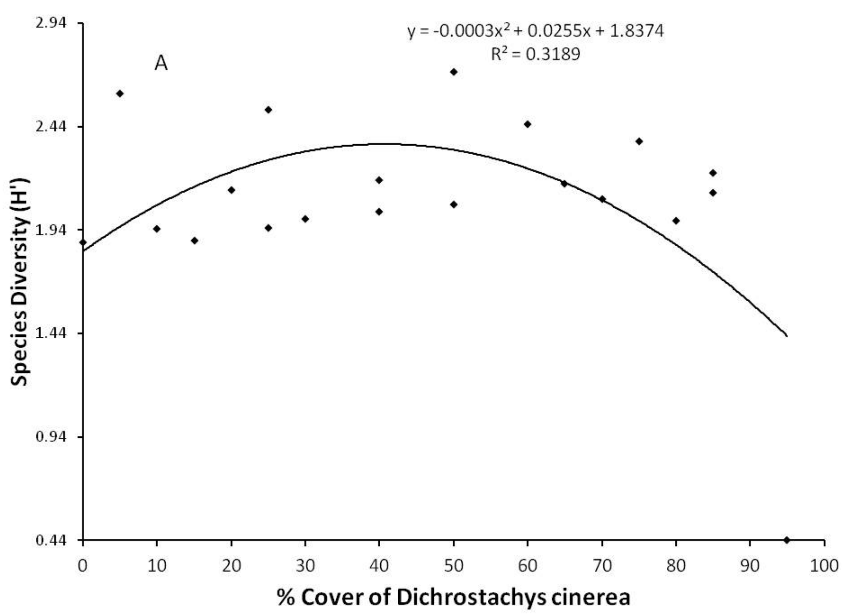

Figure 9: Species diversity (H') per 10m X 10m plots in relation to cover of *D. cinerea*. The solid line shows a significant regression (*P*<0.05). (Source: Field data, 2011)

Pattern of vegetation composition along the gradient of D. cinerea.

Detrended Correspondence Analysis (DCA) was performed to study the pattern of species distribution along the gradient of *D. cinerea*. The DCA resulted in a total of 3 Axes and is summarized in Table 4. Total inertia indicates the total variation in the data set. The length of gradient is the total length of the axis before and after rescaling and scaled into units that are the average standard deviation of species turnover (SD units). The more SD units that occur along the axis the more change in species composition shown. The DCA results indicate fairly long gradients of axis 1 (2.45 SD) and axis 2 (2.19 SD). A quite high proportion (96%) of the species variation can be explained by the axis 1 and axis 2. This gives a good spatial distribution of the species along the axes.

Table 4: Results from DCA, including Eigen values, gradient length, and total inertia

	DCA axis		
	1	2	3
Eigen Value	0.62	0.34	0.13
Length of gradient (sd)	2.45	2.19	1.67
Total inertia		2.75	

Figure 10 shows the DCA diagram for the species along the *D. cinerea* gradient. The distance between the species indicates the degree of similarity in patterns of abundance and distribution. Species located near each other in the ordination space will have a more similar distribution than species far apart.

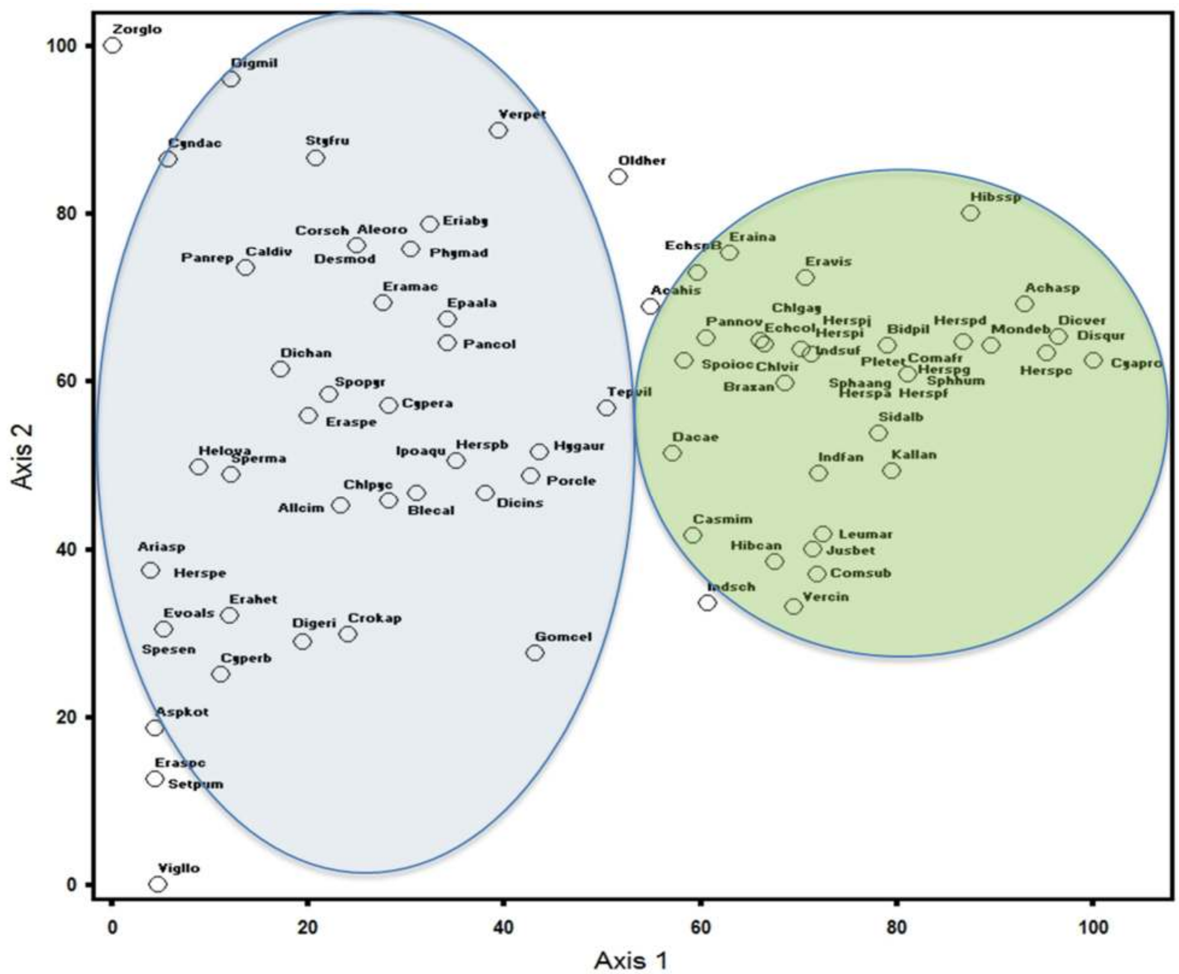

Figure 10. Ordination of all plant species in the plots using DCA with PCORD. Circles indicate the species in the diagram. The different species occurring with exactly the same abundances in the same plot occupy the same point on the diagram. The distances between points on the graph represent the distribution of species. Full names of all the abbreviated species are indicated in appendix 3. (Source: Field data, 2011)

The different communities are dispersed along the two main axes of DCA (Figure 10, Axis 1 = 62% of variance explained, Axis 2 = 34% of variance explained). Along the first axis the plant communities found in dense stands of *Dichrostachys cinerea* appear on the extreme right (in the green ellipse) and includes plant species, such as *Sida alba, Achyranthes aspera* and *Dicliptera verticillata*.

Some species, such as *Eragrostis viscosa, Dichantium insculptum*, *Blepharis colonuera, Oldenladia herbacea, Epaltes alata, Panicum novermnerve* and *Sporobolus ioclados,* show an intermediate position and dominant in plots that are of medium to dense cover.

Plant communities on the left occur in low and moderately encroached sites (in the blue ellipse). This community includes plant species such as *Dicanthium insculptum, Cynadon dactylon, Digitaria milanjiana. Eragrostis inamoena, Vigna longifolia*, *Digitaria eriantha*, *Zornia glochidiata, Eragrostis heteromera* and *Epaltes alata.* Axis 2 in the DCA is of more difficult interpretation.

The sequences of species composition along the *D. cinerea* gradient suggest that plant vegetation composition changes with the increasing cover of *D. cinerea*

Impact of increasing cover of M. pigra on plant species richness and diversity

A total of 28 plant species were recorded along the *M. pigra* gradient, 13 grasses and 15 forbs (Appendix 4). Species richness ranged from 2 to 14 species per plot. With an increase in the cover of *M. pigra*, plant species richness along the gradient decreased significantly (r^2=0.25, p=0.03) (Figure 11a). Species richness in the densest shrublands was throughout lower than in the open grasslands. There was no relationship between plant species diversity (H') (r^2 =0.04, p= 0.41), number of forbs (r^2=0.08, p=0.254) and increasing cover of shrubs. The number of grass species showed a marginally significant quadratic relationship (r^2=0.28, p=0.08) (Figure 11b). The number of grass species tended to decline with increasing *M. pigra* cover. Only two (2) grass species, *Echinocloa pyramidalis* and *Paspalidium obtusifolium*, were found at 98-100% cover respectively (figure 11b).

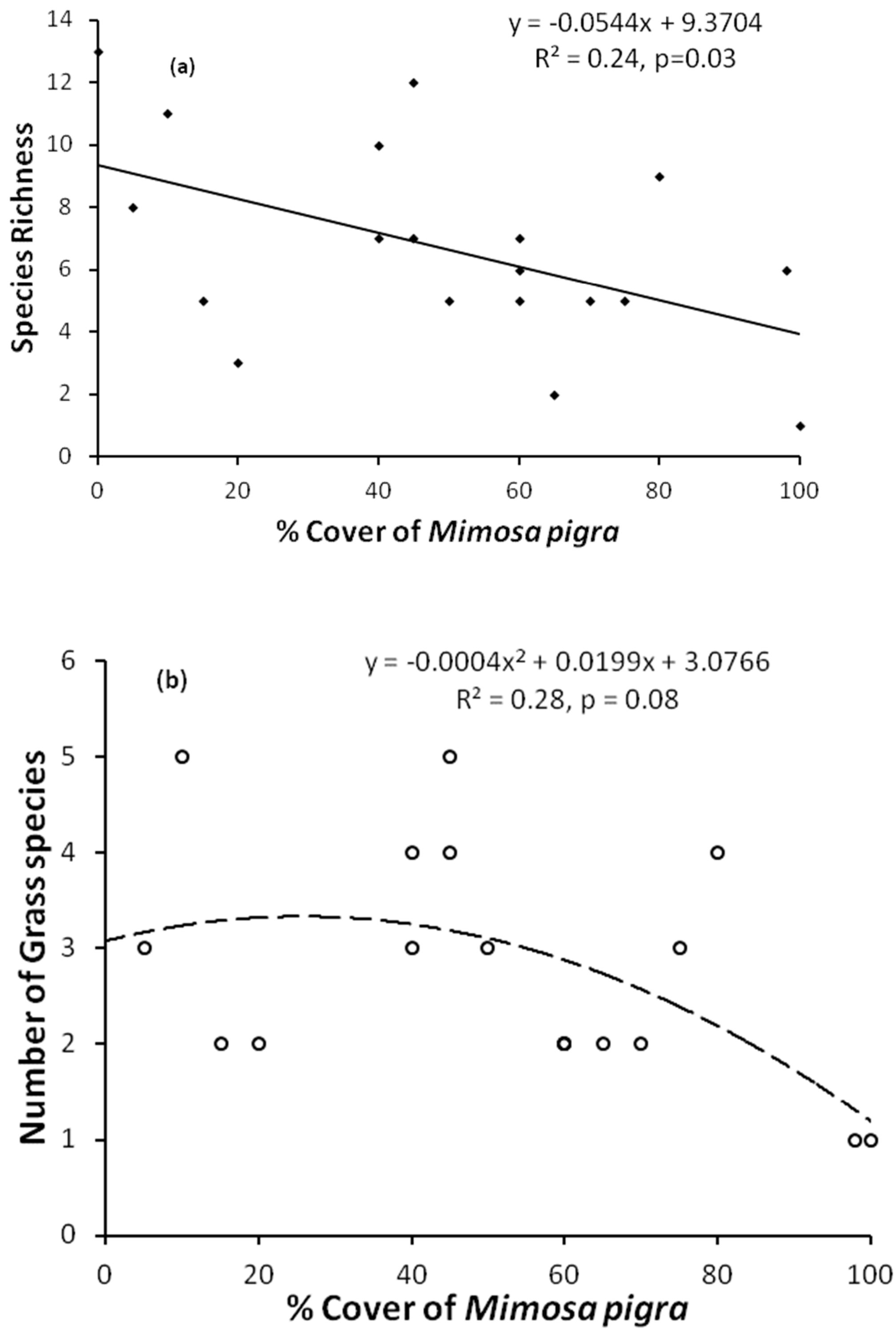

Figure 11. (a) Species richness and (b) number of grass species per 10 x 10m plots in relation to cover of *M. pigra*. (Source: Field data, 2011)

Understory vegetation distribution along the gradient of M. pigra.

Detrended Correspondence Analysis (DCA) resulted in a total of 3 Axes and is summarized in Table 5

Table 5 Results from DCA, including Eigen values, gradient length, and total inertia

	DCA axis		
	1	2	3
Eigen Value	0.84	0.47	0.11
Length of gradient (sd)	3.27	3.26	1.8
Total inertia		2.88	

The above table shows that a high proportion (84%) of the variation in axis one is explained. And cover of *M. pigra* determines this variation in species occurrence. Along the first axis the plant communities found in dense stands of *M. pigra* appeared on the extreme right (in the brown ellipse) and included plant species; *Vossia cuspidata, Oryza longistaminata and Sacciolepis Africana* (Figure 12). Some species; *Eleocharis dulcis, Leersia denudata and Echinocloa pyramidalis* showed an intermediate position and dominant in plots that were of medium shrub cover. Plant communities on the left occurred in low encroached sites (in the blue ellipse). This community included plant species; *Cynodon dactylon, Paspalidium obtusifolium, and Echinocloa stagnina* (Figure 12). Axis 2 is of more difficult interpretation. The sequences of species composition along the *M. pigra* gradient suggest that plant vegetation composition changes with increasing cover of *M. pigra.*

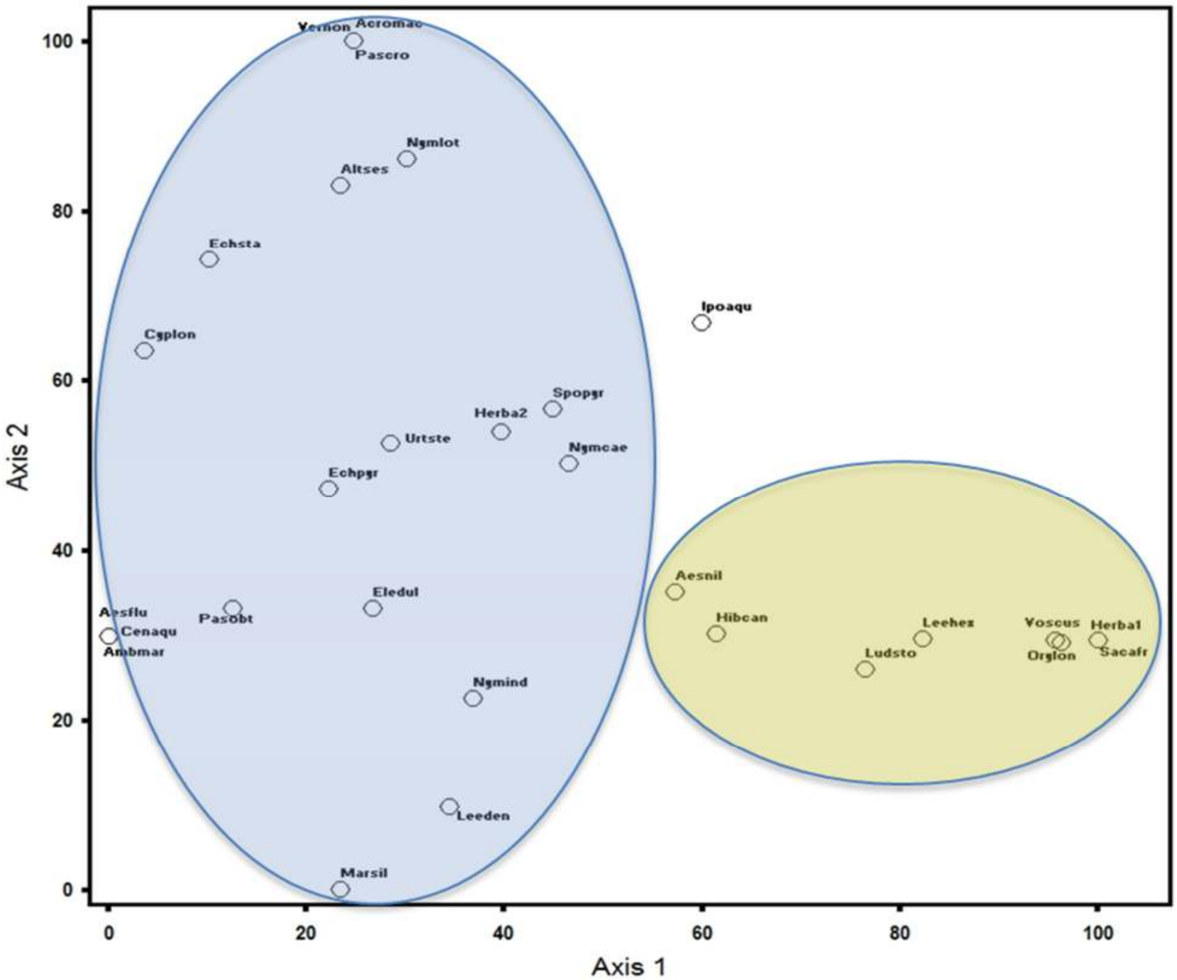

Figure 12. Ordination of all plant species in the plots using DCA with PCORD. Circles indicate the species in the diagram and the triangles are the plots. The different species occurring with exactly the same abundances in the same plot occupy the same point on the diagram. The distances between points on the graph represent the distribution of species. Full names of all the abbreviated species are indicated in Appendix 4. (Source: Field data, 2011)

5.3 Impact of Shrub Encroachment on Food Supply for Herbivores.

5.3.1 Understory Vegetation Cover

Grass cover declined with increasing shrub cover in both *D. cinerea* gradient (r^2 =0.68, p<0.001) and *M. pigra* (r^2=0.28, p=0.02) gradients. In the *D. cinerea* gradient, cover of grass particularly decreased above a shrub cover of 30-40% (Figure 13a). Grass cover in the densest *M. pigra* shrublands was throughout lower than in the open grasslands (Figure 13b). Increasing shrub cover had no significant impact on cover of forbs for both *D. cinerea* (r^2 = 0.098, p=0.18) and *M. pigra* gradients (r^2=0.08, p=0.254).

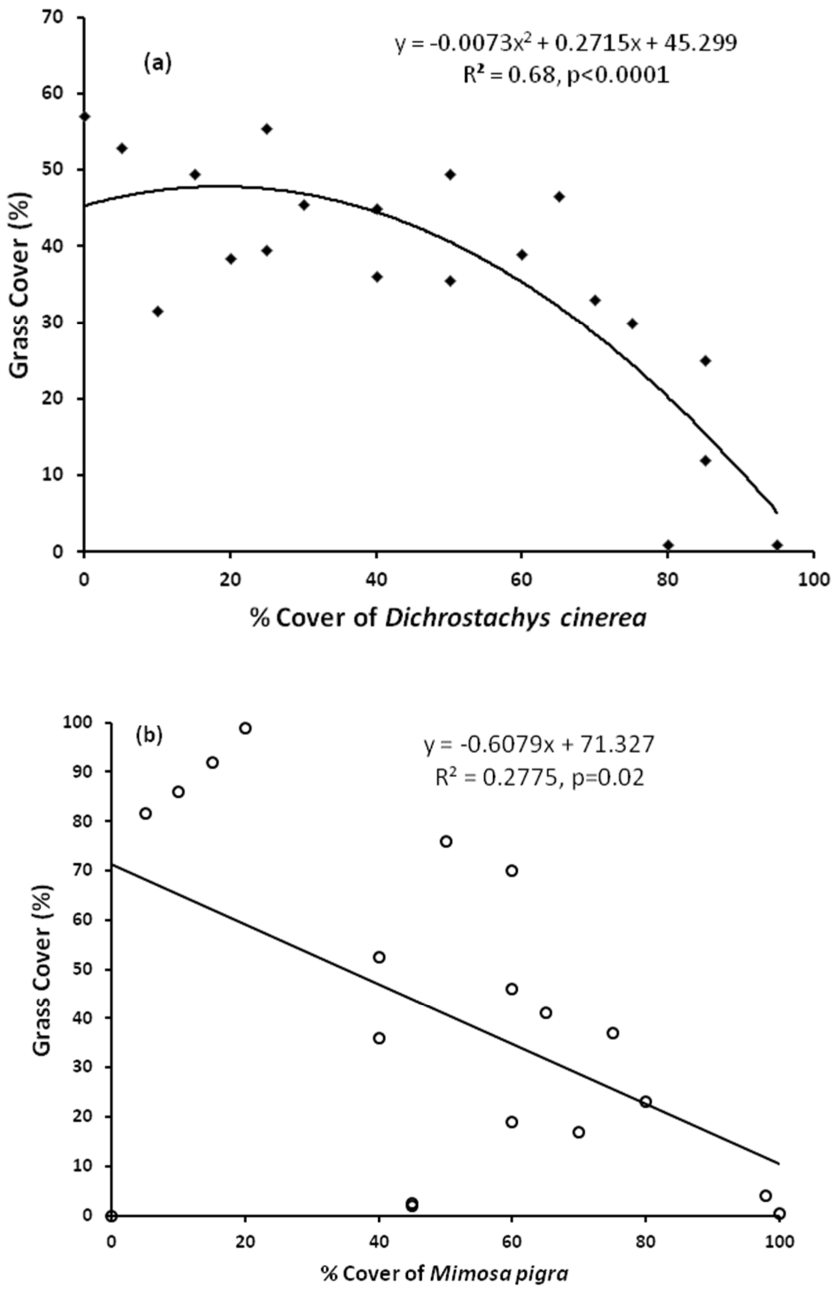

Figure 13.Relationships between grass cover and shrub cover of (a) D. *cinerea* and (b) *M. pigra.* Note that the Y-axis scales differ among the panels. (Source: Field data, 2011)

5.3.2 Plant Biomass Production

Total standing biomass in December 2010 and the herbage production between mid-November and end of December 2010 tended to decrease with increasing cover of *D. cinerea* (Figure 14A, 14B). Also, standing biomass and production of grasses decreased along the gradient (Figure 14C, 14D).

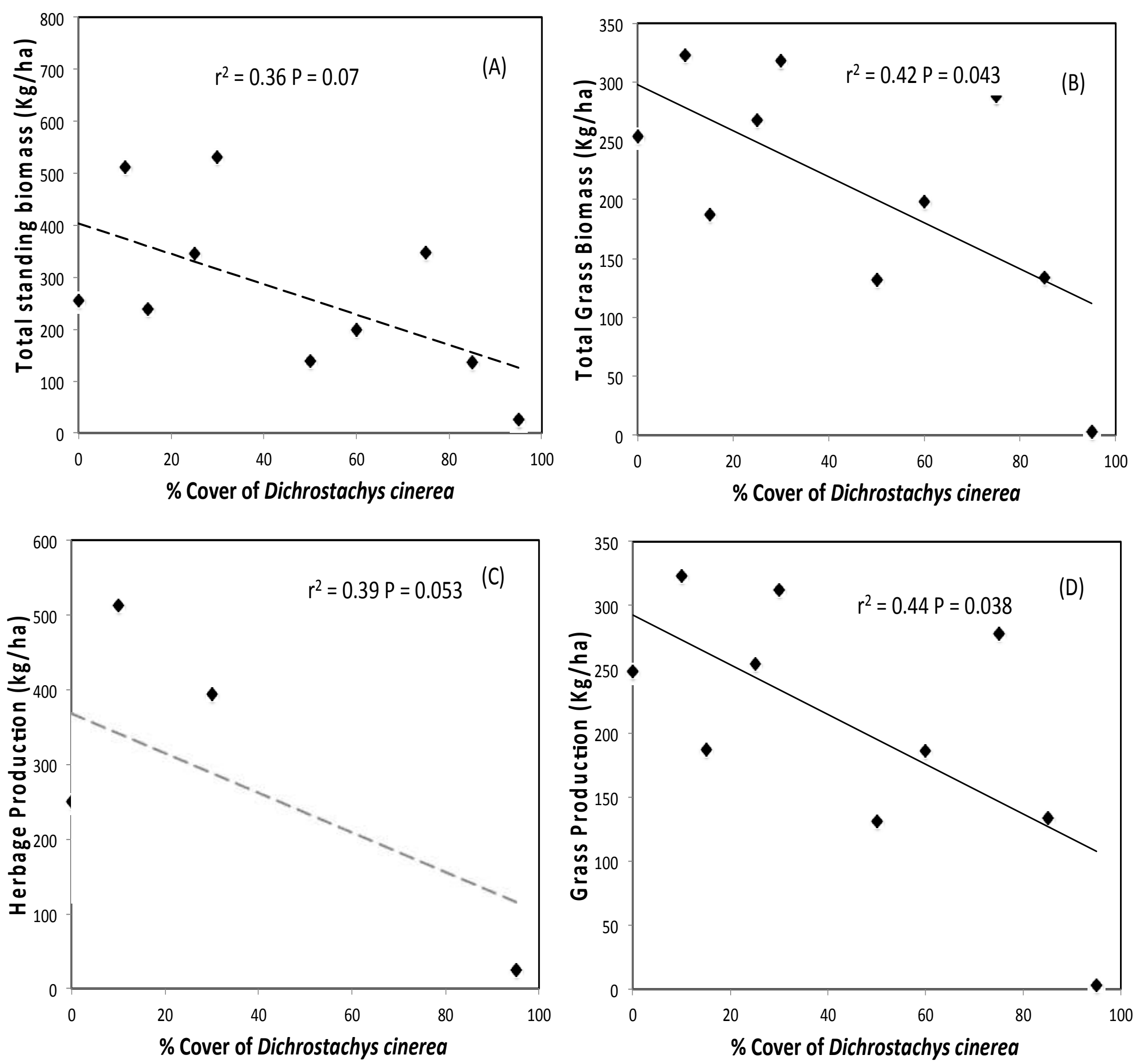

Figure 14: Total standing biomass and biomass production of the total herbaceous vegetation (A, B) or only grasses (C, D) in relation to cover of *D. cinerea*. The solid line shows a significant regression (P<0.05); the dashed line shows a trend (0.1<P<0.05). The Y-axis scale differs among panels. (Source: Field data, 2010)

In the *M. pigra* gradient, the total standing biomass as well as grass biomass peaked at intermediate shrub cover (Figure 15A, 15C). Drastic reductions in grass biomass occurred in sites greater than 50% shrub canopy cover (Figure 15A, 15C). Herbage production showed a linear decrease with increasing canopy cover of *M. pigra* (Figure 15B) whilst no significant impact on grass production existed (Figure 15D).

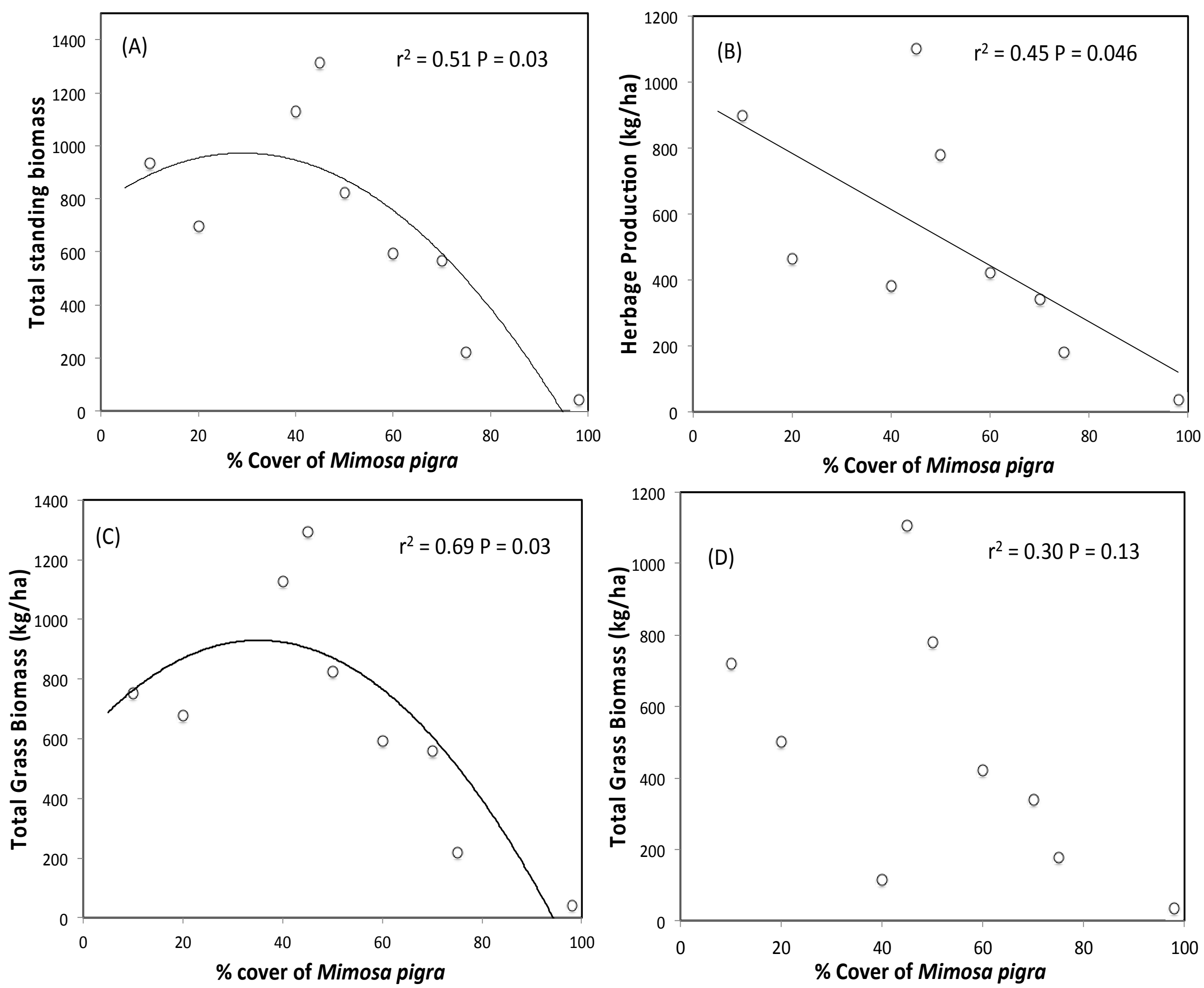

Figure 15: Total standing biomass and biomass production of the total herbaceous vegetation (A, B) or only grasses (C, D) in relation to cover of *M. pigra*. The solid lines show significant regressions (P<0.05). The Y-axis scale differs among panels. (Source: Field data, 2011)

5.3.3 Herbage Quality

In the *D. cinerea* gradient, the concentrations of both phosphorous (Figure 16a) and nitrogen (Figure16b) in aboveground grasses strongly increased with increase of *D. cinerea* cover. There was no significant relationship with the concentrations of phosphorous (r^2= 0.006, p=0.51) and nitrogen (r^2= 0.001, p=0.92) along the *M. pigra* gradient (Figure 16b and 16c, respectively). The nitrogen and phosphorous ratio showed no relationship with increasing cover of *D. cinerea* (r^2=0.01, p=0.72) and increasing cover of M. pigra (r^2=0.04, p=0.58).

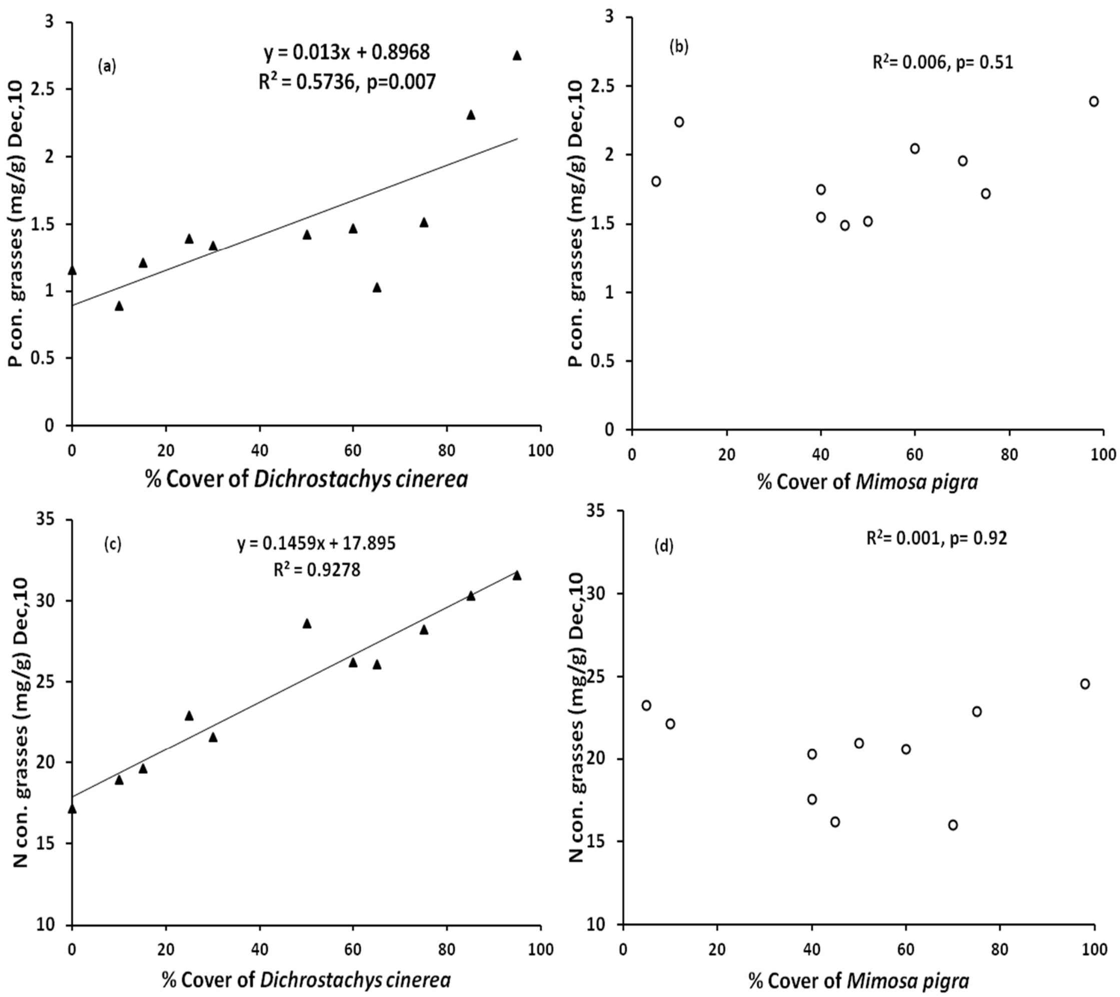

Figure 16: Relationship between N and P concentration in the grass biomass along the shrub cover gradient of *D. cinerea* and *M. pigra* sites. (Source: Field data, 2011)

CHAPTER SIX: DISCUSSION

6.1 Impact of Shrub Encroachment on Soil Nutrient Properties

Result of a literature review by Ehrenfeld (2003) suggested that when an N_2-fixing species invades a community in which N_2-fixers are absent or rare, there is likely to be large changes in many aspects of both carbon and nitrogen dynamics. Further, the presence of N_2-fixing species in invaded or encroached ecosystems could increase soil nitrogen and carbon pools (Resh et al. 2002; Liao et al. 2008; McKinley and Blair 2008). In this study all measured soil nutrient concentrations increased significantly with increase in the cover of *D. cinerea* showing that soil fertility under *D. cinerea* cover improves. Soil carbon also increased significantly along the shrub cover gradient of *D. cinerea*. These results are consistent with similar studies elsewhere in savanna grasslands where soils under woody vegetation had higher carbon (Hudak et al. 2003) and increased soil nutrient concentrations compared to open sites (Ludwig et al. 2004; Hudak et al. 2003). The increase in total nitrogen is likely a result of nitrogen fixation associated with *D. cinerea* (Sprent 2009) that is followed by nitrogen enrichment of the soils through decomposition and leaf litter (Baer et al. 2006; Treydte et al. 2007). Nitrogen fixing plants produce large quantities of nitrogen rich litterfall that may rapidly increase nitrogen and also carbon cycling (Brantley and Young 2008)

It is believed that N_2-fixing trees might have a higher requirement for soil phosphorous (Vitousek et al. 2002), and thus, the expectation of this study was to find low levels of phosphorous in dense stands of N_2-fixing plants. Treydte et al. (2007) indeed observed lower levels of soil phosphorous found underneath canopies of N_2-fixing acacias than in open sites in a Tanzanian savanna. However, in this study a significant increase in the soil phosphorous pool and plant available phosphorous along the gradient from open grasslands to dense *D. cinerea* stands was observed. The increase of the soil phosphorous pool may result from the exploitation of phosphorous from deeper soil layers that the woody plants explore, as has been observed in some previous studies (Ludwig et al. 2004; Belsky et al. 1989; Bate and Gunton 1982 cited in Dunham 1991; Sitters et al. in press).

Given that *M. pigra* is also an N_2-fixing shrub, it was expected that the increase in *M. Pigra* cover would lead to an increase in the total soil carbon and nitrogen pools and a reduction in soil phosphorous pools. Results in this study, however, did not support these expectations. No relationship existed between the measured soil variables with an increase in the cover of *M. pigra*. These findings could be as a result of an already elevated level of Soil C, N and P in the soils along the selected cover gradient. The floodplain areas where *M. pigra* encroaches are characterised by deep cracking montmorillonite clay soils. Studies have shown that soils with a higher silt and clay content enable fine textured soils to accumulate and retain more carbon and nitrogen (Hudak et al. 2003). Organic carbon and nutrient enrichment, as a result of sedimentation after flooding events (Pinay et al. 1992; Olde Venterink et al. 2006), partly explains the elevated levels of carbon and nitrogen along the entire *M. pigra* gradient. Results of a comparison in mean concentrations of nutrients in this study show that there are different trends in soil nitrogen, phosphorous and carbon along the *D. cinerea* and *M. pigra* gradients. This can, at least partly, be explained by the different background levels of soil carbon and nitrogen between the two gradients. Along the *M. pigra* gradient soil carbon and nitrogen pools were 5-10 times larger than in the *D. cinerea* gradient. And so increases in the nitrogen and carbon pools due to the shrub encroachment are strongly influenced by dissimilarities in the areas in which *M. pigra* and *D. cinerea* encroaches. Thus, this result shows that shrub encroachment of an N_2-fixer in an already nitrogen and carbon rich environment has a smaller impact in the ecosystem functioning than in a poorer environment.

6.2 Impact of Shrub Encroachment on Plant Species Diversity and Vegetation Composition.

The second objective of this study was to show how encroachment of shrubs affects species diversity and vegetation composition. This study showed that plant species richness and diversity reduces with increasing cover *D. cinerea*. A significant hump-backed relationship existed between species diversity and richness (though marginally) and cover of *D. cinerea*. A similar pattern was found in other areas where species richness and diversity exhibited a hump-backed relationship with increasing cover of shrubs (Isermann et al. 2007). These results agree with the habitat heterogeneity hypothesis (MacArthur and Wilson 1967). The intermediate part of the shrub gradients provided both niches for open savanna conditions and woodland conditions. Other studies on woody plant encroachment (Lett and Knapp 2005; Price and Morgan 2008; Baez and Collins 2008) found a negative correlation between increasing shrub cover and species richness of the understory vegetation. The species richness of grasses in particular decreased significantly above 40% shrub cover indicating a threshold level at which many grasses are unable to persist. Changes in the microenvironment associated with the presence of *D. cinerea* likely influenced the species richness and composition of the understory flora, with declines evident where the shrub canopy formed a dense closed stratum. The observed environmental variable associated with increasing cover of *D. cinerea* was a significant reduction in light intensity beneath the shrub canopy. Reductions in light intensity below the shrub canopy have been found to reduce species richness (Hobbs and Mooney 1986; Price and Morgan 2008). Shading can affect the germination and establishment of herbaceous species (Morgan 1998 cited in Morgan and Price 2008) and light penetrating through the shrub canopy may influence the differential ability of species to establish (Morgan and Price 2008). The DCA showed that vegetation composition changes with an increase in the cover of *D. cinerea*. Plant species common in the open sites did not occur in very dense sites and vice versa. Dense shrub cover favoured shade tolerant grasses and shade tolerant forbs as shown in the DCA diagram. *Mimosa pigra* cover along the gradient was associated with significant reductions in plant species richness. Shifts in understory vegetation composition were also evident and this is also attributed to the shading as a result of increased cover of *M. pigra.*

The alteration of species composition as a result of encroaching shrubs may have a direct influence on the food availability for grazers. Kafue lechwe diet studies by Rees in 1978 and Handlos et al, in 1976 showed the preferred plant species that constituted the major food source for the Kafue lechwe in the termitaria and floodplain grassland. Grass species affected by the encroachment of the shrubs include *Acrocerus macrum, Chloris gayana, Chloris pycnothrix, Digitaria milanjiana, Echinochloa colona, Echinochloa stagnina, Leersia denudata and Sporobolus pyramidalis.* These grasses were excluded in dense *M. pigra* or *D. cinerea* stands whilst they occurred in open sites. Grasses such as *Panicum novermnerve, Chloris virgata, Eragrostis viscosa, Brachiaria xantholueca, Dichanthium insculptum* etc occurred along the entire gradient but where not recorded in Rees (1978) or Handlos et al. (1976). Further, additional Kafue Lechwe diet studies need to be undertaken to determine if the diet of the Kafue Lechwe has adapted to changes in vegetation composition brought about by the encroachment of the shrubs particularly in the termitaria zone where *D. cinerea* continues to encroach.

6.3 Impact of Shrub Encroachment on Food Supply for Large Herbivores.

The third objective of this study was to determine the impact of encroachment of *M. pigra* and *D. cinerea* on the food supply for large herbivores, and in particular the Kafue Lechwe. This study showed that shrub encroachment by *M. pigra* or *D. cinerea* both drastically reduced the cover, standing biomass and production of grasses. In the *D. cinerea* gradient, total standing biomass and grass biomass showed a curvilinear relationship with cover. Biomass increased initially and showed drastic reductions in sites greater than 50% shrub canopy cover showing that areas with few shrubs have a less negative effect on grass biomass than areas with dense cover of shrubs. These results are consistent with other studies that have shown a negative relationship between shrub density and grass productivity (Scholes and Archer 1997). The drastic reduction in the grass production and cover has a direct and negative influence on the food availability for grazers. The observed suppression in productivity of the encroached sites could be as a result of low irradiance and competition between the shrubs and grasses for below ground resources (Scholes and Archer 1997). Light measurements in this study showed that as shrub cover increases, light reaching the ground reduced. These results are in agreement with studies by Scholes (2003) and Ludwig et al. (2004) that showed that dense woodlands tend to decrease grass cover and productivity due to decreased light intensity.

The results, however, also showed that the herbage quality, in terms of nitrogen and phosphorous concentrations in grass biomass, increases with the increase of *D. cinerea* cover. This study showed that nitrogen and phosphorous concentrations are increased by a factor of 2 to 3 along the *D. cinerea* gradient. Similar results elsewhere in African savannas also showed that grasses growing under and around tree canopies had a much higher forage quality than grasses from open grasslands (Treydte et al. 2007; Ludwig et al. 2008). The herbage quality is probably caused by the increased soil nitrogen and phosphorous pools and availabilities along the *D. cinerea* gradient (Olff et al. 2002; Ludwig et al; 2008). The higher forage quality could partly be caused by an alteration in grass species composition. However, since dominant species such as *Panicum novermnerve*, *Sporobolus ioclados*, *Echinocloa colona*, *Chloris virgata*, *Eragrostis viscosa* and *Brachiaria xantholueca* occurred along the entire shrub gradient this is likely not the most prominent cause of the higher forage quality under dense *D. cinerea* stands. The negative effects of high shrub cover on grass quantity and availability may also counteract any positive effects of high shrub cover on grass quality. Noteworthy, it was recently observed that the Kafue lechwe have started to eat the seedpods of *D. cinerea* as they pass through the termitaria zone during their annual migration from the high areas to the floodplain during the months of May to July (Peter 2011). In these months, when food supply is at its lowest, these seedpods may constitute a large proportion of the Lechwe diet (Peter 2011). It requires further study to evaluate how much the consumption of seedpods of *D. cinerea* can compensate for the loss of grasses during this period of food scarcity, how this supply of seedpods is influenced by the shrub encroachment, or even how the consumption of seedpods by the Lechwe may influence the spatial distribution of *D. cinerea*.

A study by Blaser et al. (in press) showed that in the period 2008-2010 approximately 2000 ha (or 19%) out of an area of approximately 10500 ha of floodplain grassland in Lochinvar National Park were covered by sparse and dense *M. pigra* stands. Because it forms thick and impenetrable shrubs (Shanungu 2009), *M. pigra* prevents the use of the invaded areas for grazing by the lechwe. In the termitaria grasslands, 28% of the total area (approximately 6800 ha) was encroached by *D. cinerea*, which has become prominent and forms thickets. Although *D. cinerea* forms thickets similar to *M. pigra*, there are spaces in the understory where grasses still grow and lechwe can access these grasses, and as described above, the loss of grass production may, at least partly, be compensated by increased quality. Nevertheless, the encroachment of *M. pigra* and that of *D. cinerea* is likely to have a direct negative influence on the lechwe population. Significant proportions of the areas previously available for grazing are lost and this has a resultant effect of reducing the carrying capacity of the grasslands of Lochinvar National Park to support large concentrations of lechwe. Additionally, the exclusion nature of the shrubs has resulted in the displacement of the lechwes away from the national parks in to the Game Management Areas (GMA) where they receive less protection and thus susceptible to poaching (Shanungu 2009).

A study by Genet (2007) determined that the grasslands (both floodplain and termitaria) are continuously being replaced by the shrubs at a rate of 228 ha per year. Blaser et al. (in press) determined a combined rate of encroachment of *M. pigra*, *D. cinerea* and *Acacia* species of approximately 130 ha per year (based on satellite images from 1994-1995 and 2008–2010). The rate at which the grasslands of Lochinvar National park are being encroached with shrubs is alarming. At these rates of encroachment, much of the suitable habitat for lechwe within Lochinvar National Park will be occupied by the shrubs and further reduce availability of grazing ground on which the lechwe populations solely depend. From this study, there was no negative feedback for the *D. cinerea* encroachment because of the reduced soil phosphorous availability, therefore, it cannot be expected that this encroachment has reached its final expansion. Thus expansion of *D.cinerea* in the study area will continue to occur as it is most likely determined by the flooding conditions and not necessarily soil nitrogen and phosphorous availabilities.

CHAPTER SEVEN: CONCLUSION AND RECOMENDATIONS

7.1 Conclusion

The study aimed at showing impacts of the encroachment of *D. cinerea* and *M. pigra* on various ecosystem functions of the Floodplain and termitaria grasslands of Lochinvar National Park. The first hypothesis that shrub encroachment increases soil nitrogen and carbon pools but leads to a reduction in soil phosphorous pools is not supported. It is not possible to make a generalized conclusion about the overall impact of shrub encroachment as the individual species have specific impacts to the ecosystem. Overall, this study showed that encroachment of *D. cinerea* shrubs not only increased the soil pools of nitrogen and carbon, as could be expected, but also that of phosphorous. The increase of soil phosphorous indicates that the encroachment of *D. cinerea*, so far, did not experience a negative feedback because a limited availability of phosphorous might limit growth and N-fixation of the leguminous shrubs. However, the encroachment of *M. pigra* did not alter the soil condition.

The second hypothesis that shrub encroachment reduces plant species diversity and changes the composition of the understory vegetation is supported. The encroachment of *D. cinerea* and *M. pigra* significantly impacted species richness and diversity of plants and the vegetation composition of the understory.

The third hypothesis that shrub encroachment reduces biomass production of the understory vegetation, and that this would lead to a reduction in food supply for large herbivores particularly the Kafue Lechwe, is supported in this study. The study showed that both species largely reduced cover of grasses and grass biomass production. This suggests that shrub encroachment has reduced food for grass-eating herbivores, particularly the endemic Kafue lechwe, in Lochinvar National Park.

Furthermore, results of soil nutrient study, as well as an analysis of shrub encroachment based on satellite images show that this shrub encroachment has likely not reached its end yet, and hence the Kafue Flats are themselves being destroyed and degraded, and not only the lechwe but also eventually the cattle industry that depend on the extensive floodplains will be negatively impacted in the future.

7.2 Recommendations and Management Implication

This research is one step ahead in building on ecological studies associated with the problem of shrub encroachment and its impacts in grassland ecosystems. It will be a basis for continuing with research on this subject matter on the wider areas of the Kafue flats and beyond. Based on the findings of this research, the following recommendations are made:

1. Lochinvar National Park is a world-renowned bird sanctuary. The focus of this study was on impacts of shrub encroachment on ecosystem functioning and plant species diversity as well as impacts on herbivore food supply. However, further research is needed to determine the impacts of shrub encroachment on bird species diversity and composition as a result of the changed habitat conditions.

2. This study showed that encroachment of shrubs creates significant problems for wildlife conservation especially those that depend on the extensive grasslands for their survival. The reduction in the cover of palatable grasses and subsequent reductions in herbage production as a result of the increase of shrub cover profoundly affects grassland management. Shrub invaded grasslands can no longer support high numbers of Kafue Lechwe, which are the traditional grazers the Kafue Flats floodplains. It is thus recommended that control of the spread of shrubs particularly *Mimosa pigra* be continued. The study showed that the *M. Pigr*a does

not alter the soil nutrient properties and thus the areas occupied with *M. pigra* have a high likelihood of being restored to pre-encroached conditions.

3. Anecdotal reports indicate that there has been an increase in the sighting of browsers such as Kudu and Impala in the termitaria grasslands - in the areas that are invaded by *D. cinerea*. This suggests that encroachment of shrubs and woody species such as *D. cinerea* and acacias has created a habitat for browsers and mixed feeders. It is thus recommended that Government should consider the introduction of other browsing ungulates to the park and to also re-introduce some mammal species that were previously known to occur here such as Sable (*Hippotragus niger*) and Eland (*Taurotragus oryx*). Such a management action could reduce the rate of encroachment of *D. cinerea* and *Acacia* species and increase the animal spectrum of the park and enhance the development of tourism.

REFERENCES

Adams, B. W., O. Castelli, F.G. Gardner, G. Cartwright, and J. Clark. 1992. Fire and grazing to manage willow shrubland on foothill range. *Pub No. T/207*. Edmonton, Alberta, Canada. Range Notes 15:1–6.

Adeel, Z. 2008. Findings of the Global Desertification Assessment by the Millennium Ecosystem Assessment – A Perspective for Better Managing Scientific Knowledge. In: *Future of Drylands* (eds Lee, C. and Schaaf, T.). UNESCO, Paris, pp. 677–685.

Allen S. E., (ed). 1989. *Chemical Analysis of Ecological Materials, 2nd edition. Blackwell Scientific Publishers*. Oxford, UK. 386p.

Archer S., Schimel D. S. and Holland E. A. 1995. Mechanisms of shrubland expansion: land use, climate or CO2? *Clim.Change* 29, 91–9.

Baer S.G., Church J.M., Williard K.W.J., Groniger J.W. (2006). Changes in intrasystem N cycling from N2-fixing shrub encroachment in grassland: multiple positive feedbacks. *Agr Ecosyst Environ* 115:174-182

Baez, S. and Collins, S.L. 2008. Shrub invasion decreases diversity and alters community stability in northern Chihuahuan desert plant communities. *PLoS ONE*, 3, 2332.

Belsky, A. J. 1992. Effects of trees on nutritional quality of understorey gramineous forage in tropical savannas. *Tropical Grasslands* **26**:12-20.

Belsky AJ, Amundson RG, Duxbury JM, Riha SJ, Ali AR, Mwonga SM. 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *J Appl Ecol* 26:1005–1024.

Binkley D and Matson P. 1983. Ion exchange resin bag method for assessing forest soil nitrogen availability. *Soil Science Society of America Journal* 47: 1050–1052

Blaum N., Seymour C., Rossmanith E., Schwager M., and Jeltsch F. 2009. Changes in arthropod diversity along a land use driven gradient of shrub cover in savanna rangelands: identification of suitable indicators. *Biodivers Conserv* 18:1187–1199

Bond, W. J., G. F. Midgley, and F. I. Woodward. 2003. The importance of low atmospheric CO2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* **9**:973-982

Bork E.W. and A.M. Burkinshaw. 2009. Cool-Season Floodplain Meadow Responses to Shrub Encroachment in Alberta. *Rangeland Ecology and Management* 62(1), pp. 44 – 52.

Brantley S.T. and Young D.R. 2008. Shift in litterfall and dominant nitrogen sources after expansion of shrub thickets. *Oecologia* 155:337-345.

Bray, R. H. and L. T. Kurtz. 1945. Determination of total, organic and available phosphorus in soils. *Soil Science* **59**:39-45

Buckley, Y. M., Rees, M., Paynter, Q., and Lonsdale, M. 2004. Modelling integrated weed management of an invasive shrub in tropical Australia. *Journal of Applied Ecology*, 41(3), 547-560.

Cabral, A.C., De Miguel, J.M., Resicia, A.J., Schmitz, M.F., and Pineda, F.D. 2003. Shrub encroachment in Agentinean Savannas. *Journal of Vegetation Science* 14: 145 – 152.

Chabwela, H. N. W. and W. Mumba. 1998. Case Study: Zambia.Integrating Water Conservation and Population. *Strategies on the Kafue Flats*.

Coetzee, B.W.T., Tincani, L., Wodu, Z. and Mwasi, S.M. 2008. Overgrazing and bush encroachment by *Tarchonanthus camphoratus* in a semi-arid savanna. *Afr. J. Ecol*., 46, 449–451.

D' Odorico, P., Fuentes, J.D., Pockman, W.T., Collins, S.L., He, Y., Medeiros, J.S. 2010. Positive feedback between microclimate and shrub encroachment in the northern Chihuahuan desert. *Ecosphere*, 1, Article 17, doi: 10.1890/ES10- 00073.1

Douthwaite, R.J. and van Lavieren, L.P. 1977. A description of the Vegetation of Lochinvar National Park, Zambia. *National Council for Scientific Research*. Zambia, NCSR/TR 34, 66pp

Dunham K. M. 1991. Comparative effects of Acacia albida and Kigelia Africana trees on soil characteristics in Zambezi riverine woodlands. *Journal of Tropical Ecology*, vol. 7, No.2. pp 215-220.

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6: 503–523.

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

Ellenbroek, G.A. 1987. Ecology and productivity of an African wetland system. The Kafue Flats. Zambia. *Dr. W. Junk Publishers*. The Netherlands. 267 pp

Genet, B. S. 2007. *Shrub Encroachment into Grassland and its Impact on Kafue Lechwe in Lochinvar National Park, Zambia*. MSc. Thesis. ITC, Enschede, The Netherlands

Gylstra, M.L.D., Y. Hussin and C.B. Mwasile. 2008. Remote Sensing for integrated Water Resources Management in Kafue Flats Zambia. Arnhem, the Netherlands. xi + 44pp.

Handlos, D. M., W. L. Handlos, and Howard, G.H. 1976. A Study of the Diet of the Kafue Lechwe (Kobus Lechwe) by Analysis of Rumen Contents. *Proceedings of the Fourth Regional Wildlife Conference for Eastern and Central Africa*. Department of National Parks and Wildlife Service, Lusaka. Pp. 197-211.

Hagenah N., Munkert H., Gerhardt K., Olff H. 2009. Interacting effects of grass height and herbivores on the establishment of an encroaching savana shrub. *Plant Ecology*. 201: 553-566.

Haubensak, K.A. and Parker, I.M., 2004. Soil changes accompanying invasion of the exotic shrub Cytisus scoparius in glacial outwash prairies of western Washington [USA]. *Plant Ecology*, 175(1), p.71-79

Hibbard K. A., Archer S., Schimel D. S. and Valentine D. V. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology.*

Hill, M.O and Gauch. H. G. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47-5882, 1999–2011

Hobbs, R. J., and H. A. Mooney. 1986. Community changes following shrub invasion of grassland. *Oecologia* 70:508–513.

Hudak A. T., C. A. Wessman and T. R. Seastedt. 2003. Woody overstorey effects on soil carbon and nitrogen pools in South African savanna.

Isermann M., M., Diekmann and S.,Heemann. 2007. Effects of the expansion by *Hippophaë rhamnoides* on plant species richness in coastal dunes. *Applied Vegetation Science*, 10(1):33-42. 2007.

Kampamba G. and V. R. Nyirenda. 2004. *Pilot Surveys: Instruments and tools for assessing the Environmental and Social-economic Impact of Invasive Alien Plant Species.* Final report, Environmental Council of Zambia (ECZ), Lusaka.

Kent, M. and P. Coker. 1992. Vegetation Description and Analysis: a Practical Approach. John Wiley and Sons, New York, NY, USA.

Knapp, A.K., Briggs, J.M., Collins, S.L., Archer, S.R., Bret-Harte, M.S., Ewers, B.E. 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Glob. Change Biol.*, 14, 615–623.

Koerselman W, Meuleman AFM. 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *J Appl Ecol* 33:1441–1450

Leonard, P. 2005. *Important bird areas in Zambia.* The Zambia Ornithological Society. MRM Graphics, Singapore. Pp. 85.

Lett M. S. and Knapp A. K. 2005. Woody Plant Encroachment and Removal in Mesic Grassland: Production and composition responses of herbaceous vegetation. *American Midland Naturalist*, Vol. 153, No. 2 pp. 217-231

Lonsdale W. M., I. L. Miller, and I.W. Forno. 1989. The Ecology of Australian Weeds 20: *Mimosa Pigra L. Plant Protection Quarterly*, 4: 119 – 131.

Ludwig, F., de Kroon, H., Berendse, F., Prins, H.H.T. 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecol*. 170, 93–105.

Ludwig, F., H. De Kroon, H.T. Prins. 2008. Impacts of Savanna trees on forage quality for a large African Herbivore. *Oecologia* 155: pp 487 – 496.

MacArthur R. H. and Wilson O. E. 1967. The theory of island biogeography. Princeton University Press, Princeton

McCune, B. and M.J. Mefford. 2006. PC-ORD. Multivariate Analysis of Ecological Data. Version 5.10. MjM Software, Gleneden Beach, Oregon, USA.

McKinley, D. C., and Blair, J. M. 2008. Woody Plant Encroachment by Juniperus virginiana in a Mesic Native Grassland Promotes Rapid Carbon and Nitrogen Accrual. *Ecosystems*, *11*(3), 454–468. doi:10.1007/s10021-008-9133-4.

McNaughton S.J., D.G. Milchunas., and D.A. Frank. 1996. How can net Primary Productivity be measured in Grazing Ecosystems? *Ecology* vol 77, issue 3. Pp 974-977.

Minnesota Department of Natural Resources. 2007. *A handbook for collecting vegetation plot data in Minnesota: The relevé method.* Biological Report 92. St. Paul: Minnesota Department of Natural Resources.

Miller I.L., and Pickering S.E. 2001. *M. pigra* or Giant Sensitive Plant (Mimosa pigra). *Agnote*. Weeds Branch, Darwin, Australia

Montane, F. Rovira, P., and Casals, P. 2007. Shrub encroachment into mesic mountain grasslands in the Iberian peninsula : Effects of plant quality and temperature on soil C and N stocks, *21*, 1-10.

Mueller-Dombois D. and Ellenberg V. 1974. The count-plot method and plotless sampling techniques. In: *Aims and Methods of Vegetation Ecology* pp. 96–108. John Wiley and Sons, New York

Mumba, M., and J. R. Thompson. 2005. Hydrological and Ecological Impacts of Dams on the Kafue Flats Floodplain System, Southern Zambia. *Physics and Chemistry of the Earth* 30:442-447

Oba, G., Post, E., Syversten, P.O., and Stenseth, N.C., 2000. Bush cover and range condition assessments in relation to landscape and grazing in Southern Ethiopia. *Landscape Ecology* 15, 535–546.

Olde Venterink, H., Vermaat, J. E., Pronk, M., Wiegman, F., van der Lee, G. E., van den Hoorn, M. W., Higler, L. and Verhoeven, J. T. 2006. Importance of sediment deposition and denitrification for nutrient retention in floodplain wetlands. Applied Vegetation Science, 9: 163-174.

Olff, H., F. Berendse, and W. Devisser. 1994. Changes in nitrogen mineralization, tissue nutrient concentrations and biomass compartmentation after cessation of fertilizer application to mown grassland. *Journal of Ecology* **82**:611-620.

Orwa, C.; Mutua, A.; Kindt, R.; Jamnadass, R.; Anthony, S. 2009. Agroforestree Database: a tree reference and selection guide version 4.0. World Agroforestry Centre, Kenya

Pajunen, A. M., Oksanen, J., and Virtanen, R. 2011. Impact of shrub canopies on understorey vegetation in western Eurasian tundra, 1-10. doi:10.1111/j.1654-1103.2011.01285.x

Paynter, Q., and Flanagan, G. J. 2004. Integrating herbicide and mechanical control treatments with fire and biological control to manage an invasive wetland shrub, *Mimosa pigra*, 615-629.

Paynter Q, Flanagan G. J., Lonsdale W. M., Schatz T, and Steinbauer M. J. 2000. Ecological Studies to Optimise the Integrated Management of the Wetland Weed*, Mimosa Pigra. In Proceedings of the 10th international symposium on the Biological Control of the weeds*; 4 – 14 July, 1999. Montana State University, Bozeman, Montana, USA.

Peter F. 2011. *The Role of Lechwe Antelopes in the Expansion of the Native Legume Shrub Dichrostachys cinerea in Lochinvar National Park, Zambia*. MSc.Thesis in Environmental Sciences. Swiss Federal Institute of Technology (ETH) Zurich

Pinay G, Fabre A, Vervier P, Gazelle F.1992. Control of C, N, P distribution of riparian forests. *Landscape Ecology* 6, 121-132.

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

Rees W.A. 1978. The Ecology of the Kafue Lechwe: Its Nutritional Status and Herbage Intake. *Journal of Applied Ecology*, Vol. 15, No 1, pp. 193 – 203.

Resh, S. C., Binkley, D., and Parrotta, J. A. 2002. Greater Soil Carbon Sequestration under Nitrogen-fixing Trees Compared with Species. *Ecosystems*, *5*(3), 0217–0231. doi:10.1007/s10021-001-0067-3.

Riginos, C., J. B. Grace, D. J. Augustine, and T. P. Young. 2009. Local versus landscape-scale effects of savanna trees on grasses. *Journal of Ecology* **97**:1337-1345

Roques, K.G., O_Connor, T.G. and Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *J. Appl. Ecol*., 38, 268–280.

SAS Institute. 2006. JMP 5.0.1.2 SAS Institute, Cary, North Carolina, USA.

Sayer J. A and Van Lavieren L.P. 1975. The ecology of the Kafue lechwe population of Zambia before the operation of hydro-electric dams on the Kafue River. *E Afri. Wild. J*. Vol 13, 9-37

Scholes R.J. 2003. Convex Relationships in Ecosystems Containing Mixtures of Trees and Grass. *Environmental and Resource Economics* 26: 559–574, 2003

Scholes R.J. and S.R. Archer. 1997. Tree-Grass Interactions in Savannas. *Annual Review of Ecology and Systematics*, Vol. 28, pp. 517 – 544.

Sirami C., Seymour C., Midgley G., and Barnard P. 2009. The impact of shrub encroachment on savanna bird diversity from local to regional scale. *Diversity and Distributions* 15, 948–957

Sitters, J., P. J. Edwards, and H. Olde Venterink. 2013. Increases of soil C,N and P pools along *Acacia* tree gradients and their feedbacks on trees and grasses. *Ecosystems*.

Shanungu, G. K. 2009. Management of the invasive *Mimosa pigra L*. in Lochinvar National Park, Zambia. *Biodiversity* (Ottawa) 10:56-60

Shanungu, G. K., and Blaser W.J. 2011. *Lochinvar National Park: Distribution and population estimates of Large Mammals and the Status of Mimosa pigra invasion*. Technical Report. Department of Research, Zambia Wildlife Authority, Chilanga

Smith T., Mlambo V., Sikosana N.L.J., Maphosa V., Mueller-Harvey I., Owen E. 2005. *Dichrostachys cinerea* and *Acacia nilotica* fruits as dry season feed supplements for goats in a semi-arid environment: Summary of a DFID funded project in Zimbabwe. Animal Feed Science and Technology. 122 (2005) 149 – 157.

Sprent J.I. 2009. Legume Nodulation: *Global Perspective*. Oxford: Wiley-Blackwell.

Storrs, A.E.G. 1995. Know Your Trees: *Some of the common trees found in Zambia. Regional Soil Conservation Unit*, (RSCU).

Ter Braak C.J.F. 1987. Unimodal models to relate species to environment. Dissertationsthesis landbouwenuniveriteitete Waageningen, Waageningen

TexaSoft. 2007. WINKS SDA Software, 6th Edition, Cedar Hill, Texas,.

Thomas, I. J. 2007. *Mapping and Modeling of Mimosa pigra Expansion in Lochinvar National Park, Zambia*. MSc. Thesis. ITC, Enschede, The Netherlands.

Treydte, AC, I.M.A Heitkonig, Prins H.T, Ludwig F. 2007. Trees improve grass quality for herbivores in African savannas. *Perspective in Plant Ecology, Evolution and Systematics* 8 (2007) 197 – 205

Trollope, W.S.W., Hobson, F.O., Danckwerts, J.E. and Van Niekerk, J.P. 1989. *Encroachment and control of undesirable plants. Veld Management in the Eastern Cape* (eds J.E. Danckwerts and W.R. Teague), pp. 73–89. Department of Agriculture and Water Supply, Pretoria, South Africa.

Turner, B. 1985. *Map of Lochnivar National Park.* Kafue Basin Research Project. University of Zambia, Lusaka

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* **31**:197-215.

Van Auken, O.W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. *J. Environ. Manag*., 90, 2931– 2942.

Vitousek, P.M., Cassman, K., Cleveland, C., Crews, T., Field, C.B., Grimm, N.B., Howarth, R.W., Marino, R., Martinelli, L., Rastetter, E.B., Sprent, J.I. 2002. Towards an ecological understanding of biological nitrogen fixation. *Biogeochemistry* 57/58, 1–45.

Yusuf H., Trydete A.C, Demissew S., Woldu Z. 2011. Assessment of woody species encroachment in the grasslands of Nechisar National Park, Ethiopia. *African Journal of Ecology*. 49: 397-409.

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

White, R.P., Murray, S., Rohweder, M. (2000). *Pilot analysis of global ecosystems: grassland ecosystems*. World Resources Institute, Washington,DC.

Whittaker, R. H. (1972). Evolution and measurement of species diversity. Taxon, 21 (2), 213-251.

.

LIST OF APPENDICES

Apendix 1. Relevee recording sheet.

Date **Releve Nr**

Coordinates N E

Aspect /type

Description / Remarks

vegetation height (cm)		average:	max:
	Herb layer		
	Shrub layer		

Water depth (cm)		Quadrat size (m2)	
Vegetation cover (%)			

	Species Name	description	Specimen Nr	Cover %	Cover class
1					
2					
3					
4					
5					
6					
7					
8					
9					
10					
11					
12					
13					
14					
15					
16					
17					
18					
19					
20					

Termite Mounds
Cover sum:
Number of species:

Appendix 2: Vegetation composition along the shrub cover gradient of *D. cinerea*. The numbers in the table represents the cover of the species in 10m X 10m plots. The plots are arranged in ascending order of shrub cover and grouped into four groups.

			Open to moderate dense shrubland							Moederately dense shrubland					Moderate to dense shrubland				Dense shrubland			
		Plot ID	G6	G14	G21	G23	G20	G15	G12	G1	G13	G3	G24	G11	G18	G25	G5	G7	G22	G19	G8	G2
		Canopy cover	0	5	10	15	20	25	25	30	40	40	50	50	65	70	70	75	80	85	85	95
	Species Name	Functional Group																				
1	*Blepharis calonuera*	Forb	2	5	6	4	1	3	20	5		1		2	1	2		2	<1	<1	<1	<1
2	*Panicum novermnerve*	Grass	4	2	2	1	2	1	4	3	15	4	5	2	2	5	1	<1		4	4	<1
3	*Sporobolus ioclados*	Grass	30	20	1	15	20	30		25		5	20	4	8	8	25	4	<1	10	8	
4	*Tephrosia villosa*	Forb		<1	<1	<1	<1	<1	<1	2.5	<1	<1		3	1		<1	<1		<1		<1
5	*Vernonia cinerea*	Forb	4						5						<1		2	1	2		<1	<1
6	*Eragrostis viscosa*	Grass	2	2	2	<1	<1	2.5	1	2		2	4		2		8			4		
7	*Brachiaria xantholueca*	Grass		2.5			<1			<1		<1		1	<1	1	<1			2		
8	*Hygrophylla auriculata*	Forb	3	3		8	3	5	10	20	10		5	3	5	8	2.5	3	<1			
9	*Indigofera fanshaweii*	Forb	<1			<1		<1											<1			
10	*Hibiscus canabinus*	Forb							2	2		<1								2		
11	*Commelina subulata*	Forb							<1	<1		<1		<1								<1
12	*Chloris virgata*	Grass	2					1		<1	2		2				2.5	2		4		
13	*Cassia mimosoides*	Forb				<1	<1		<1			<1		<1	<1	<1				<1		
14	*Echinocloa colona*	Grass		4											1			1	<1	1		
15	*Vernonia petersii*	Forb		1	20	<1	2			<1	<1	5	20		2		1		1			
16	*Dichanthium insculptum*	Grass	15	5		25	5	15	1	8	2	<1		20	20	8	1	20				
17	*Eragrostis inamoena*	Grass	<1	4	<1	1			<1				2.5	<1	5	5	<1					
18	*Eriospermum abysinicum*	Forb		<1	<1		<1	<1	<1				<1	<1	<1		<1					
19	*Chloris pycnothrix*	Grass	1	1		<1		<1	4	1	10		1	5		2		1				
20	*Crotalaria kapiriensis*	Forb		<1			<1		2			<1		<1	<1		<1	<1				
21	*Digitaria eriantha*	Grass		1				1	4			2.5			2			1				
22	*Gomphrena celosioides*	Forb	<1						<1									1				
23	*Epaltes alata*	Forb		15	4	2	4	4			45	15	2	10	20	15						
24	*Eragrostis heteromera*	Grass	1	1	1	5	8		15		2	20		4		1						
25	*Stylosanthes fruticosa*	Forb	<1	<1	2		<1	<1	<1				<1	<1	1							
26	*Oldenlandia herbacea*	Forb		<1	<1		<1	<1					<1		<1	<1						
27	*CyperaceaA*	Grass		<1		<1		<1							<1							
28	*CyperaceaB*	Grass	<1						2		1			<1								
29	*Digitaria Milanjiana*	Grass			20					5						1						
30	*Sporobolus pyramidalis*	Grass				1					1				1							
31	*Alloteropsis cimicina*	Grass					<1		1		<1	<1		<1	4							
32	*Acanthospermum hispidum*	Forb									<1						<1					
33	*Porphyrostemma clevalieri*	Forb						1						<1			<1					
34	*Chloris gayana*	Grass						4					1			2						
35	*Eragrostis spc*	Grass							4					2								
36	*Aspilia kotchya*	Forb							<1					<1								
37	*Setaria pumila*	Grass							2					1								
38	*Spermacoce*	Forb	<1								2			2								
39	*Dichandria*	Grass		4			1				2			2								
40	*Cynodon dactylon*	Grass		2	5				1			1		5								
41	*Helliotropium ovalifolium*	Forb									<1			<1								
42	*Dactyloctenium aegyptium*	Grass									<1						<1	<1				
43	*Justicia betonica*	Forb										1		<1			<1	2	1			
44	*Hibiscus sp*	Forb											<1						1			
45	*Echinocloa spB (perenial)*	Grass								<1	4											<1
46	*Sida alba*	Forb									<1				<1		1	1	<1		<1	<1
47	*Dicliptera verticillata*	Forb											5		2	25	4	2	15	16	4	75
48	*Achyranthes aspera*	Forb											<1						1	2	1	2
49	*Bidens pilosa*	Forb													1				<1	<1		
50	*Kalanchoe lanceolata*	Forb															<1	<1	<1			
51	*Leucas martinicensis*	Forb																4			2.5	
52	*Monechma debile*	Forb																	<1	1		
53	*Cyathula prostrata*	Forb																			<1	1
54	*Eragrostis macilenta*	Grass	1	4																		
55	*Alectra orobanchoides*	Forb		<1																		
56	*Corchorus schimperi*	Forb		<1																		
57	*Desmodium*	Forb		<1																		
58	*Zornia glochidiata*	Forb			<1																	
59	*Eragrostis spe (small)*	Grass					1															
60	*Herb spb*	Forb						<1														
61	*Ipomea aquatica*	Forb						<1														
62	*Vigna llongifolia*	Forb							<1													
63	*Phyllanthus maderaspatensis*	Forb								<1												
64	*Calostestophana divaricata*	Forb									<1											
65	*Panicum repens*	Grass									5											
66	*Evolvulus alsinoide*	Forb										2.5										
67	*Spermatococe senensis*	Forb										<1										
68	*Aristida sp*	Grass												2								
69	*Herb spe*	Forb												1								
70	*Panicam coloratum*	Grass													<1							
71	*Herb spi*	Forb															<1					
72	*Herb spj*	Forb															<1					
73	*Indigofera suffruticosa*	Forb															<1					
74	*Indigofera schimperi*	Forb																1				
75	*Disperma quadrangulare*	Forb																	<1			
76	*Herb spc*	Forb																	<1			
77	*Herb spd*	Forb																		1		
78	*Commelina africana*	Forb																			<1	
79	*Herb spa*	Forb																			1	
80	*Herb spf*	Forb																			<1	
81	*Herb spg*	Forb																			1	
82	*Plectranthus tetragonus*	Forb																			<1	
83	*Sphaeranthus angolensis*	Forb																			<1	
84	*Sphaeranthus humilis*	Forb																			1	

Appendix 3. Name of the species displayed in Figure 10 (DCA diagram for *D. cinerea*)

No.	Abbreviation	Species	
1	Blecal	*Blepharis*	*calonuera*
2	Pannov	*Panicum*	*novermnerve*
3	Spoioc	*Sporobolus*	*ioclados*
4	Tepvil	*Tephrosia*	*villosa*
5	Vermin	*Veronica*	*cinerea*
6	Travis	*Eragrostis*	*viscosa*
7	Braxan	*Brachiaria*	*xantholueca*
8	Hygaur	*Hygrophylla*	*auriculata*
9	Indfan	*Indigofera*	*fanshaweii*
10	Chlvir	*Chloris*	*virgata*
11	Casmim	*Cassia*	*mimosoides*
12	Echcol	*Echinocloa*	*colona*
13	Verpet	*Vernonia*	*petersii*
14	Dicins	*Dichanthium*	*insculptum*
15	Eraina	*Eragrostis*	*inamoena*
16	Eriaby	*Eriospermum*	*abysinicum*
17	Chlpyc	*Chloris*	*pycnothrix*
18	Crokap	*Crotalaria*	*kapiriensis*
19	Digeri	*Digitaria*	*eriantha*
20	Gomcel	*Gomphrena*	*celosioides*
21	Epaala	*Epaltes*	*alata*
22	Erahet	*Eragrostis*	*heteromera*
23	Styfru	*Stylosanthes*	*fruticosa*
24	Oldher	*Oldenlandia*	*herbacea*
25	Sperma	*Spermacoce*	
26	Dichan	*Dichandria*	
27	Cyndac	*Cynodon*	*dactylon*
28	Cypera	*CyperaceaA*	
29	Cyperb	*CyperaceaB*	
30	Zorglo	*Zornia*	*glochidiata*
31	Digmil	*Digitaria*	*Milanjiana*
32	Spopyr	*Sporobolus*	*pyramidalis*
33	Allcim	*Alloteropsis*	*cimicina*
34	Acahis	*Acanthospermum*	*hispidum*
35	Porcle	*Porphyrostemma*	*clevalieri*
36	Chlgay	*Chloris*	*gayana*
37	Eraspc	*Eragrostis*	*spc*
38	Aspkot	*Aspilia*	*kotchya*
39	Setpum	*Setaria*	*pumila*
40	Helova	*Helliotropium*	*ovalifolium*
41	Dacae	*Dactyloctenium*	*aegyptium*
42	Jusbet	*Justicia*	*betonica*
43	Hibcan	*Hibiscus*	*canabinus*

44	Hibssp	*Hibiscus*	*sp*
45	Comsub	*Commelina*	*subulata*
46	EchspB	*Echinocloa*	*spB*
47	Sidalb	*Sida*	*alba*
48	Dicver	*Dicliptera*	*verticillata*
49	Achasp	*Achyranthes*	*aspera*
50	Bidpil	*Bidens*	*pilosa*
51	Kallan	*Kalanchoe*	*lanceolata*
52	Leumar	*Leucas*	*martinicensis*
53	Mondeb	*Monechma*	*debile*
54	Cyapro	*Cyathula*	*prostrata*
55	Eramac	*Eragrostis*	*macilenta*
56	Aleoro	*Alectra*	*orobanchoides*
57	Corsch	*Corchorus*	*schimperi*
58	Desmod	*Desmodium*	
59	Eraspe	*Eragrostis*	*spe*
60	Herspb	*Herb*	*spb*
61	Ipoaqu	*Ipomea*	*aquatica*
62	Vigllo	*Vigna*	*llongifolia*
63	Phymad	*Phyllanthus*	*maderaspatensis*
64	Caldiv	*Calostestophana*	*divaricata*
65	Panrep	*Panicum*	*repens*
66	Evoals	*Evolvulus*	*alsinoide*
67	Spesen	*Spermatococe*	*senensis*
68	Ariasp	*Aristida*	*sp*
69	Herspe	*Herb*	*spe*
70	Pancol	*Panicum*	*coloratum*
71	Herspi	*Herb*	*spi*
72	Herspj	*Herb*	*spj*
73	Indsuf	*Indigofera*	*suffruticosa*
74	Indsch	*Indigofera*	*schimperi*
75	Disqur	*Disperma*	*quadrangulare*
76	Herspc	*Herb*	*spc*
77	Herspd	*Herb*	*spd*
78	Comafr	*Commelina*	*africana*
79	Herspa	*Herb*	*spa*
80	Herspf	*Herb*	*spf*
81	Herspg	*Herb*	*spg*
82	Pletet	*Plectranthus*	*tetragonus*
83	Sphaang	*Sphaeranthus*	*angolensis*
84	Sphhum	*Sphaeranthus*	*humilis*

Appendix 4 Vegetation composition along the shrub cover gradient of *M. pigra*. The numbers in the table represents the cover of the species in the 10m X 10m plots

					Open to moderate dense				Moderately dense					Moderately to very dense						Very dense		
			Plot ID	**EF12**	**MG18**	**MG1**	**MG17**	**MG20**	**MG2**	**MG6**	**MG5**	**MG14**	**MG16**	**MG7**	**MG19**	**MG21**	**MG11**	**MG13**	**MG3**	**MG12**	**MG4**	**MG10**
			Canopy Cover		**5**	**10**	**15**	**20**	**40**	**40**	**45**	**45**	**50**	**60**	**60**	**60**	**65**	**70**	**75**	**80**	**98**	**100**
No.	**Species Name**	**Abbreviation**	**Functional Group**																			
1	*Urticularia stellaris*	Urtste	Forb	0.5	0.5	0.5			2	0.5	0.5		0.5	0.5							0.5	0.5
2	*Oryza longistaminata*	Orylon	Grass			1		98	5					4		45	40	15	10	16		
3	*Paspalidium obtusifolium*	Pasobt	Grass	70	0.5	80			20	10	0.5	0.5	2	15	60				2	1	4	
4	*Nymphea caerulea*	Nymcae	Forb		0.5	5	1	1	5	15	3	6	3	6	4	1		1	4	0.5	2	
5	*Ipomea aquatica*	Ipoaqu	Forb		0.5	1	0.5		1	0.5	2		0.5	1	0.5	0.5		2	0.5	0.5	1	
6	*Aeschynomene nilotica*	Aesnil	Forb	0.5		0.5			0.5			0.5								0.5		
7	*Ludwigia stolonifera*	Ludsto	Forb	0.5	4							0.5				4		8		0.5		
8	*Alternanthera sessilis*	Altses	Forb								0.5										0.5	
9	*Hibiscus sp*	Hibcan	Forb	0.5		0.5														0.5		
10	*Nymphea lotus*	Nymlot	Forb	0.5	5						15			4	1							
11	*Leersia denudata*	Leeden	Grass		80	1	90	1	25	25		1	70		10			2	25			
12	*Herb 2 (floating hydrophyte)*	Herba2	Forb						0.5	1				1								
13	*Eleocharis dulcis*	Eledul	Grass		1	2	2		2.5	1	0.5	0.5										
14	*Echinocloa stagnina*	Echsta	Grass	0.5		2					1											
15	*Nymphoides indica*	Nymind	Forb	0.5		2			30													
16	*Aeschynomene fluitans*	Aesflu	forb	0.5																		
17	*Ambrosia maritima*	Ambmar	forb	0.5																		
18	*Centrostachys aquatica*	Cenaqu	Forb	0.5																		
19	*Leersia hexandra*	Leehex	Grass	0.5			0.5															
20	*Acrocerus macrum*	Acromac	Grass								0.5											
21	*Cyperus longus*	Cyplon	Grass	3							0.5											
22	*Paspalum scrobiculatum*	Pascro	Grass								0.5											
23	*Vernonia sp*	Vernon	Forb								0.5											
24	*Sporobolus pyramidalis*	Spopyr	Grass									0.5										
25	*Sacciolepsis africana*	Sacafr	Grass													1						
26	*Herb 1*	Herba1	Forb													1						
27	*Vossia Cuspidata*	Voscus	Grass														1			4		
28	*Echinochloa pyramidalis*	Echpyr	Grass																		0.5	

Appendix 5. Preferred grasses for Kafue Lechwe on the Kafue Flats (Data from Handloss *et al*, 1976 and Rees, 1978).

Plant name	**Handlos & Howard**	**Rees**
Acroceras macrum	x	x
Aescynomene fluitans	x	
Brachiaria latifolia = B. arrecta	x	
Brachiaria rugulosa	x	x
Chloris gayana	x	
Chloris pycnothrix	x	
Chloris virgata	x	
Cynodon dactylon	x	
Digitaria milanjiana	x	
Digitaria ternata	x	
Echinochloa colonum/E. holibii = E.colona	x	
Echinochloa pyramidalis	x	x
Echinochloa stagnina	x	x
Eragrostis gangetica	x	
Eragrostis pilosa	x	
Eulalia geniculata = Eulalia aurea	x	
Leersia denudata	x	
Leersia freisii (Leersia denudata)	x	
Oryza Longistaminata	x	
Panicum coloratum	x	
Panicum repens		x
Panicum subalbidum	x	
Panicum trichinode	x	
paspalum orbiculare = Paspalum scrobiculatum	x	
Setaria spacellata	x	x
Sporobolus natalensis	x	
Sporobolus pyramidalis	x	
Sporobolus sp. aff. festivus	x	
Sporobolus spicatus	x	
Vetiveria nigritana	x	
Vossia cuspidata	x	x