



UPPSALA  
UNIVERSITET

## Changes in spatial structure of woody savanna vegetation after 11 years of exclusion of large herbivores



Andrea Herrera

---

Degree project in biology, Master of science (1 year), 2011

Examensarbete i biologi 30 hp till magisterexamen, 2011

Biology Education Centre and Department of Ecology and Genetics, Plant Ecology and Evolution, Uppsala University

Supervisors: Prof. Christina Skarpe, Prof. Roger Bergström, Doc. Ingvar Backéus and Dr. Moffat Setshogo

<b>Abstract</b> .....	3
<b>Introduction</b> .....	4
- General.....	4
- Plant-herbivore interaction.....	4
- Browsing effects on the vegetation structure.....	5
- Aims of the study.....	5
<b>Material and methods</b> .....	6
- Study Area.....	6
- Design of Study.....	6
- Field Methods.....	8
- Statistics.....	8
<b>Results</b> .....	10
- General.....	10
- Frequency.....	13
- Height and Canopy area.....	14
- Distribution pattern of vegetation.....	19
- Correlations.....	20
<b>Discussion</b> .....	21
- Abundance.....	21
- Height and Canopy area.....	22
- Distribution pattern of vegetation.....	23
<b>Conclusion</b> .....	23
<b>Acknowledgments</b> .....	24
<b>References</b> .....	25

## **Abstract**

The vegetation structure and the ecosystem function in the savanna are affected by several determinants, one of the major factors being herbivory. In this study the aim is to see how large herbivores affect the vegetation structure in a wooded savanna. A baseline study was conducted in 1997 in Mokolodi Nature reserve in Botswana; it included mapping and recording of all the woody plants in three different sites inside the reserve. Each of the three sites had one fenced plot to protect the vegetation from large herbivores, and one plot that were left as control plot. My study was an evaluation study that was carried out in 2007/2008. A comparison was made between the two studies and between the plots where large herbivores had been excluded and those where large herbivores were still present. The results showed no difference in stem density between the fenced and unfenced plots for all the species together, but a general increase in stem density of 63 % from 1997 to 2007/2008 was detected. *Combretum apiculatum*, *Grewia bicolor* and *Dichrostachys cinerea* were the three species with highest abundance. Only two of the most common species were affected by the exclusion of large herbivores. These are *Acacia tortilis* and *D. cinerea*, both of which were negatively affected. The exclusion of large herbivores did have a positive effect on the height and the canopy area of the trees. This evaluation study has shown that the exclusion of large herbivores has a small but significant effect on the vegetation structure, and this should be considered in areas where herbivores are declining and in park management.

*Keyword: Herbivory, animal-plant interactions, spatial distribution, woody vegetation, savanna, vegetation structure, Mokolodi Nature Reserve, Botswana*

# Introduction

## General

Savannas are tropical or near tropical ecosystems which cover large areas in Africa, South America and Australia. Savanna ecosystems are characterized by a more or less continuous herbaceous layer dominated by grasses and sedges, and discontinuous woody vegetation of trees and/or shrubs (Frost *et al.* 1986). The vegetation in the savanna is heterogeneous with trees and shrubs often forming clusters in the grassland (de Knecht *et al.* 2008). Vegetation may vary both in species composition and in structure. The spatial structure of plants can be random, regular or aggregated and may together with plant population structure and density have an effect on the function of the savanna ecosystem (Jeltsch *et al.* 1996).

The structure and dynamics of the savanna ecosystem is largely determined by soil moisture, soil nutrients, fire and herbivory (Frost *et al.* 1986, Skarpe 1992). Herbivory, including both grazing and browsing, has been shown to have major influence on the ecosystem and it is therefore of importance to study the effects of herbivory on the vegetation structure. Browsing may lead to changes in species composition, density and in the spatial structure of woody vegetation, such as height and canopy area, with consequences for further herbivory and for the ecosystem function (Adler *et al.* 2001). Therefore this subject is of interest for management and conservation issues.

The importance of large herbivores for changes in the woody component of savannas has long been studied and this is not least true for the so called bush encroachment, which is the increase of woody plants suppressing the herbaceous layer and therefore decreasing the grazing capacity of the ecosystem (Wiegand *et al.* 2005). The driving factors for bush encroachment are not well understood and still debated (Ward 2005).

## Plant-herbivore interaction

Mammals with woody plants as their main diet are called browsers and they can eat various parts of the woody plant. To minimize the negative effect of browsing on the plants, woody species have evolved tolerance or/and defense traits. A browsing tolerant species is defined as one that fast replaces the lost tissue. The reasons for the tolerance are not yet all understood. Tolerance can be inherited to the species, and/or formed by phenotypic plasticity (Bilbrough & Richards 1993). A plant's defenses to browsing can take the form of chemical defenses (compounds that are toxic or have digestibility-reducing effects) or mechanical defenses (e.g. spines and thorns), which make food intake more difficult by reducing the bite size and biting rate (Bergström 1992). Plant defenses can make a species so unpalatable that it is totally rejected or, more commonly, that it is less preferred as food. Palatable plants are those that are often preferred as food. Thus, the browsers have different preferences for different species of woody plants and different parts of the woody plant.

The different species of browsers vary in selectivity in their food intake. An extreme generalist herbivore eats plant species according to their proportions in the plant community, and an extreme specialist eats from only one species or taxonomic group of plants regardless of their proportions in the vegetation. Mammalian herbivores are usually neither extreme specialists nor generalists, and most of the browsers are selective generalists preferring some species and avoiding others (Gurevich 2002). The herbivore's selectivity is therefore important to consider in understanding the herbivore's impact on an ecosystem – an impact which can be reflected in different scales from plants to patches and landscapes. The selectivity can depend on the season. In winter and in the dry season some trees drop the leaves and the food for browsers becomes scarcer. The different woody species have different leaf falling patterns (evergreen, semi-evergreen and deciduous) in the savanna ecosystem, and this can affect the browsers' selectivity during different seasons (Edenius *et al.* 2002).

New studies show that plant-herbivore interactions also depend on the plant community context, in the way that herbivores, for example, optimize their forage intake in relation to plant species composition and food distribution. Then the spatial distribution of the woody plants has a potential effect on the foraging of browsers, meaning that neighboring plants and their differences in palatability matters for the interactions between herbivores and the vegetation (Baraza *et al.* 2006). A plant can benefit from protection by its neighbor by being associated with plants of lower palatability than its own (Hjältén *et al.* 1997). For example, palatable plants growing next to or beneath unpalatable plants with chemical or mechanical defenses may benefit, if the unpalatable plant act as a physical barrier against the herbivores. This is referred to as associative defense (Bergvall *et al.* 2008) or associational plant refuges (Hjältén *et al.* 1993). The phenomenon of associational plant refuges means that the probability of survival for an individual plant not only depends on its own characteristics but also on the characteristics and abundance of its neighboring growing plants (Hjältén *et al.* 1993).

Browsers can increase the diversity by increasing the species richness of the vegetation, if they browse on dominant species not tolerant to browsing. On the other hand, species richness can also decline if the dominant species is browsed and is tolerant to browsing (Côte *et al.* 2002). This also means that browsing can change the species composition in an ecosystem to a dominance of more browsing tolerant species.

### **Browsing effects on the vegetation structure**

Browsing by large herbivores is known to have an effect on the vegetation structure. Depending on how tolerant the plants are to browsing the stem density, frequency, and/or height can be affected to different degrees (Côte *et al.* 2002). The density and frequency can be reduced if the reproduction is negatively affected or the survival rates get lower. Compared with height of unbrowsed trees the height of browsed ones can be affected both ways resulting in taller or shorter trees. The trees can stop their growth if they put resources on other parts of the tree instead of height growth, which happens in most cases, but they can also allocate the resources to grow higher and avoid the height where they are most heavily browsed (Côte *et al.* 2002). Different species can then react in different ways or differ in their tolerance levels to browsing, but also their threshold in tolerance for browsing can differ, some species reacting sooner than others, and reacting differently depending on which life stage they are in (Hester *et al.* 2000).

Browsing does not only influence plants on an individual level but also on a community level. This may shift the community composition, often with a fast response towards a community with browsing tolerant or unpalatable species. After browsing has stopped there may be a slower response or even no response (Husheer *et al.* 2003).

### **Aims of the study**

The overall aim of this study was to find out if the exclusion of large herbivores had an impact on the structure and composition of the woody vegetation. More specifically my question is: Does exclusion of large herbivores by a fence have an impact on abundance and spatial distribution of woody plants in the savanna ecosystem? I predicted that the stem density, frequency, height and canopy area is higher in areas without large herbivore feeding than in areas where this impact does occur. Due to the experimental design I could not separate between the effects of browsers, intermediate feeders and grazers.

## Material and Methods

### Study Area

The study was done in Mokolodi Nature Reserve (24° 45' S, 25° 55' E), in south-eastern Botswana. Mokolodi is a reserve of approximately 4500 hectares, with a dominating vegetation type of mixed shrub and tree savanna (Skarpe *et al.* 2000). The vegetation in the nature reserve has been broadly divided into three vegetation zones: the combretum zone dominated by *Combretum apiculatum*, the spirostachys zone dominated by *Spirostachys Africana* and the acacia zone with *Acacia tortilis* as one of the dominant species (Skarpe *et al.* 2000). The soil in the study area is shallow and varies from sands with gravel and rock to stone-less sand. The topography of the area is moderately undulating with small hills and low mountains. The average annual rainfall in Gaborone 15 km north of the reserve is 538 mm and it falls during the wet season, summer, between November and April. The acacia zone, the most widespread vegetation lying on gentle slopes, was chosen for the study sites (Skarpe *et al.* 2000).

The area where the nature reserve now is situated used to have cattle until 1986 and was made a nature reserve in 1994. Since then the reserve has been fenced keeping the cattle out and the wild animals inside. In the reserve there is a total of 12 large herbivore species (Table 1). Of these species the main browser in the reserve is the greater kudu (*Tragelaphus strepsiceros*), other browsing species being impala (*Aepyceros melampus*), eland (*Tragelaphus oryx*), gemsbok (*Oryx gazella*), giraffe (*Giraffa camelopardalis*) (Skarpe *et al.* 2000) and four domestic, usually herded African elephants (*Loxodonta africana*).

Table 1. The 12 large herbivore species in the Mokolodi Nature Reserve. (Mokolodi nature reserve species list 2009; Kingdon 2004).

Species	Scientific name	Feeding category	Population size	Density No./km <sup>2</sup>	Body mass (kg) Female/male
<b>Impala</b>	<i>Aepyceros melampus</i>	Mixed feeder	311	6.91	40-60/45-80
<b>Greater Kudu</b>	<i>Tragelaphus strepsiceros</i>	Browser	152	3.38	120-215/190-315
<b>Wildebeest</b>	<i>Connochaetes taurinus</i>	Grazer	106	2.36	140-260/165-290
<b>Burchell's Zebra</b>	<i>Equus burchellii</i>	Grazer	74	1.64	175-250/220-322
<b>Eland</b>	<i>Tragelaphus oryx</i>	Mixed feeder	40	0.89	300-600/400-942
<b>Gemsbok</b>	<i>Oryx gazella</i>	Mixed feeder	32	0.71	180-225/180-240
<b>Giraffe</b>	<i>Giraffa camelopardalis</i>	Browser	22	0.49	450-1180/1800-1930
<b>Hartebeest</b>	<i>Alcelaphus buselaphus</i>	Grazer	22	0.49	116-185/125-218
<b>White Rhinoceros</b>	<i>Ceratotherium simum</i>	Grazer	9	0.20	1400-2000/2000-3600
<b>African Elephant</b>	<i>Loxodonta africana</i>	Mixed feeder	4	0.09	2200-3500/4000-6300
<b>Waterbuck</b>	<i>Kobus ellipsiprymnus</i>	Grazer	4	0.09	160-200/200-300
<b>Hippopotamus</b>	<i>Hippopotamus amphibius</i>	Grazer	2	0.04	510-2500/650-3200

### Design of study

An experiment was set up in 1997 in three different sites (Fig. 1) in the study area, each site with two paired plots of 150x150 m each. One of the plots in each site was fenced and this fence excluded grazing and browsing by larger herbivores. The other plot was an unfenced control plot. The plots had a buffer zone of 5.0 m from the fence or the plot border, resulting in a net study plot area of 140x140 m for each of the six plots.



Figure 1. The study area in Mokolodi Nature Reserve shown in a satellite picture from 3.22 kilometres above sea level, taken in September 2009 (Google Earth). The six plots are shown as white squares on three different sites (Site 1, Site 2 and Site 3) in the reserve. The plots with a yellow pin represent the fenced enclosure plots (plot 1, plot 3 and plot 5); the plots adjacent to the enclosure plots are the control plots (plot 2, plot 4 and plot 6).

The three sites are numbered 1-3; the six plots are numbered 1-6, the control having the even number and the enclosure having the odd number. All plots have internal coordinates based on 15 north-south lines every ten meters numbered 1-15, representing the x-coordinates, and 15 west-east lines also every ten meters named A-O, representing the y-coordinates. A subplot is then named after its north-west corner. The lines divide each plot into 196 subplots of 10x10 m. Every corner of a subplot is marked with a metal peg with a height of approximately ten cm above ground.

A baseline study was conducted in 1997 and all woody plants inside the six plots were mapped and recorded, it included a total of 1176 subplots. An evaluation study was made during winter between April and June 2007 and in summer in the end of the wet season, from February to April 2008.

My study was an evaluation of both the study in 2007 and 2008 after 11 years of treatment, i.e. exclusion of large herbivores. Due to time constraints, all subplots could not be monitored. Instead, subplots were chosen with stratified random sampling. From a list with the number of trees in each subplot from the study made in 1997, we selected the subplots which had about 25% and 75% of the maximum number of trees per plot. For the study made in 2007 the selection of subplots was made randomly.

To analyze the vegetation structure I used data from 2008 collected by me and my field study partner Hanna Leife and also the data from 2007 collected by Michaela Ditttrich. In total, data from 232 subplots from 2007 and 2008 were compared with the corresponding data from the same subplots from 1997.

## Field Methods

To locate the subplots we identified the north-south lines and west-east lines inside the plots with the help of a compass. When one metal peg in a subplot was missing, we used the surrounding pegs to establish the lost peg's position. If we could not properly identify a subplot we chose another one randomly from a pre-determined list of subplots. When a subplot was studied, the plot periphery was delineated by measuring tapes. Then four measuring tapes were placed every 2.0 m across the subplot. With help of these measuring tapes and a folding ruler we could estimate the coordinates for each individual of the woody species with an accuracy of 0.1 m.

Every tree in each subplot was mapped using a coordinate system for each subplot and recorded in the same way as in the baseline study of 1997. We measured every tree higher than 0.2 m. When trees of the same species grew close together we measured the distance between them from the periphery of the stem. If the distance was longer than 0.2 m we recorded them as two different individuals, otherwise as one individual. In the baseline study the same assumption was done but with the distance of 0.5 m between the individuals as the limit for recording the trees as one individual. On every tree selected according to the above-mentioned criteria, we did the following recordings:

- Species
- Height (from ground to highest living shoot to nearest 0.1 m)
- Canopy diameter (for both east-west and north-south direction to nearest 0.1 m)

Because of uncertainties in the identification, all the plants in the genus *Euclea* were lumped as *Euclea* spp. For individuals of the genera *Maytenus* and *Rhus* there were also some uncertainties with the identification, and these were therefore lumped as *Maytenus* spp and *Rhus* spp. Also for some of the young plants of the genera *Grewia* and *Acacia* we were not able to identify the species, and they were classified as *Grewia* sp. and *Acacia* sp.

## Statistical methods

The analyses were done on all the species grouped for each subplot, using the subplot as a unit of measure. The ten species with the highest stem density in 2007/2008 were recorded with over 300 individuals each. These ten species were then separately analyzed. The species abbreviations shown in the table 2 are used later in the graphs and figures of this paper.

Table 2. The ten species with the highest density in the study of 2007/2008 and their palatability, leaf fall pattern and mechanical defense in form of spines or thorns.

Abbreviations	Scientific names	Palatability to large herbivores	Leaf fall pattern	Mechanical defence
Ato	<i>Acacia tortilis</i>	Palatable <sup>1</sup>	Deciduous <sup>1</sup>	Spines
Cap	<i>Combretum apiculatum</i>	Palatable <sup>1</sup>	Deciduous <sup>2</sup>	No
Dci	<i>Dichrostachys cinerea</i>	Palatable <sup>1</sup>	Deciduous <sup>1</sup>	Thorns
Eri	<i>Ehretia rigida</i>	Palatable <sup>1</sup>	Deciduous <sup>1</sup>	No
Euc	<i>Euclea</i> spp	Unpalatable <sup>1</sup>	Evergreen <sup>1</sup>	No
Gbi	<i>Grewia bicolor</i>	Palatable <sup>1</sup>	Deciduous <sup>1</sup>	No
Gfl	<i>Grewia flava</i>	Palatable / Unpalatable <sup>2</sup>	Deciduous <sup>2</sup>	No
Gfv	<i>Grewia flavescens</i>	Palatable <sup>1</sup>	Deciduous <sup>1</sup>	No
Rle	<i>Rhus leptodictya</i>	Palatable <sup>1</sup>	Evergreen <sup>1</sup>	No
Saf	<i>Spirostachys africana</i>	Palatable <sup>2</sup>	Deciduous <sup>2</sup>	No

<sup>1</sup>Cooper *et al.* 1988. <sup>2</sup>Rooke 2003. <sup>3</sup>van Wyk 1997.

As the same subplots were studied in the baseline study and then 10-11 years later in our evaluation study, the subplot data are paired. To deal with the pseudoreplication, I worked with the difference for each subplot between the tree's stem density recorded in my study and that recorded in 1997. This difference was then used as data points in the tests. The study included six plots located in three different sites, with 196 subplots each plot, the evaluation study included 232 of these subplots evenly distributed between the six plots and the three sites. The vegetation at all the three sites was categorized as acacia zone in the baseline study and they were all on flat land. Since the subplots between the baseline study and the evaluation study are paired, I analyzed the subplots independently of which site they belonged to. Hence I use the subplots as a unit for statistical testing.

To test if the assumptions for parametric tests were met, I plotted the residuals and the variance of  $x$ ; I mainly focus on visual inspection. In some cases where I was not so sure I tested with the Shapiro normality test. If the assumption for a parametric test were met I used Analysis of Variance (one-way ANOVA), if not then I did a bootstrap test. I chose the bootstrap test before the non-parametric Kruskal Wallis test, since it does not rank the data as the non-parametric test does and therefore does not lose the actual values of the data points.

To analyze the abundance of the woody species I looked at the stem density which I counted as number of trees per subplot of  $100\text{m}^2$ . I then tested the differences in stem density for each subplot for all the woody species together, between the studied subplots for the control and the enclosure. The assumptions for a parametric test were met and I tested the differences in a one-way ANOVA. The same analysis was done separately for the ten most abundant species (Table 2). These were the species with the highest density in the evaluation study of 2007/2008 with a minimum of 300 trees for each species.

To see whether the frequency of species has changed between treatments from the baseline to the evaluation study, the ten most abundant species were recorded as absent (0) or present (1) in all the 232 subplots analyzed. The frequency was calculated as %, for the enclosure and control. To test if there was a change in frequency in relation to the treatment a Fisher's exact test was made.

To calculate the mean height (m) and canopy area ( $\text{m}^2$ ) in each subplot all the recorded trees in a subplot were used in the analysis. For the differences in height and canopy area a bootstrap test was used. To facilitate visual understanding the graphs are presented with ANOVA graphs. The canopy area was calculated using the recorded tree crown diameters, taking the average of the north-south and the east-west diameter, then using the area of a circle ( $r^2 \cdot \pi$ ). I also separated the trees in two height categories of trees  $\leq 1.0$  m and  $> 1.0$  m, and made a Fisher's exact test for the baseline and the evaluation study with the treatment of enclosure and control.

To see if each of the ten most abundant species were affected in height and canopy area by the treatment I subtracted the mean height and canopy area from the baseline study from those from the evaluation study in 2008 for both control and enclosure, and tested the differences in mean for each of the species. Since most of the species were not represented in all the 232 subplots, some of the subplots had one of the species missing in either the baseline study or in evaluation study in, and in some cases missing in both studies; this subplots were not included in the calculations.

The tree distribution can be analyzed by calculating the mean and the variance of the number of trees in the subplots, the mean is the mean of all the number of trees for the recorded subplots separately for 1997 and 2007/2008 and separately for the controls and the enclosure plots. The ratio of these parameters indicates the distribution pattern of the trees. If the variance to mean ratio is less than one the vegetation pattern is regular, and if the variance to mean ratio is greater than one the vegetation pattern is aggregated (Greig-Smith 1983).

For the spatial correlations between the ten most abundant species Spearman's correlation was used. They were calculated by taking the stem density per species in every subplot.

All analyses were done in R 2.7.2. The level of significance for all tests was  $\leq 0.05$

## Results

### General

In the baseline study in 1997, 42 different species of woody plants were identified and 7516 living woody plants were measured in the 232 subplots studied also in 2007/2008. In the evaluation study of 2007/2008, 47 different species of woody plants were identified and 12253 living trees were recorded and measured. Each of the studied 232 subplots analyzed was 10x10 meters, resulting in a total studied area of 23200 m<sup>2</sup>, which equals 2.32 ha.

Table 3. Woody species recorded in the 232 subplots studied in 2007/2008 and the corresponding subplots in the baseline study in 1997. The English names are from van Wyk (1997) and the names missing there were taken from Coates-Palgrave (2003). The species marked with grey were not found in the baseline study in 1997, but were recorded in 2007/2008. The species marked with pink were recorded in the baseline study but missing in the 232 subplots studied in 2007/2008. The ten most abundant species are marked with green.

Species name	Common name	Density (Trees /ha) 1997	Density (Trees /ha) 2007/2008
<i>Acacia caffra</i>	Common hook-thorn	53	59
<i>Acacia erioloba</i>	Camel thorn	0	19
<i>Acacia erubescens</i>	Blue thorn	51	70
<i>Acacia fleckii</i>	Plate thorn	0	40
<i>Acacia mellifera</i>	Black/hook thorn	14	42
<i>Acacia</i> spp.		0	21
<i>Acacia nilotica</i>	Scented thorn	58	14
<i>Acacia reficiens</i>	False umbrella thorn	0	25
<i>Acacia robusta</i>	Ankle/brack thorn	21	21
<b><i>Acacia tortilis</i></b>	<b>Umbrella thorn</b>	<b>184</b>	<b>172</b>
<i>Berchemia discolor</i>	Brown ivory/bird plum	0	4
<i>Berchemia zeyheri</i>	Red ivory	14	16
<i>Boscia albitrunca</i>	Sheperds tree	1	0
<i>Boscia foetida</i>	Smelly shepards tree	4	6
<i>Bridelia mollis</i>	Velvet bridelia	1	5
<i>Carissa bispinosa</i>	Y-thorn Carissa	<1	1
<b><i>Combretum apiculatum</i></b>	<b>Red bushwillow</b>	<b>1079</b>	<b>1331</b>
<i>Combretum hereroense</i>	Russet bushwillow	11	2
<i>Combretum imberbe</i>	Leadwood	22	21
<i>Combretum molle</i>	Velvet bushwillow	<1	3
<i>Combretum zeyheri</i>		1	0
<i>Combretum</i> spp.		0	<1
<i>Commiphora pyracanthoides</i>	Common corkwood	0	15
<i>Commiphora schimperi</i>	Glossy-leaved corkwood	40	31
<i>Croton gratissimus</i>		1	0
<b><i>Dichrostachys cinerea</i></b>	<b>Sickle bush</b>	<b>294</b>	<b>658</b>
<i>Dombeya rotundifolia</i>	Common wild pear	59	63
<b><i>Ehretia rigida</i></b>	<b>Puzzle bush</b>	<b>94</b>	<b>128</b>
<b><i>Euclea</i> spp</b>	<b>Euclea/Guarri</b>	<b>160</b>	<b>440</b>
<i>Flueggea virosa</i>	White-berry bush	2	8
<i>Gardenia volkensii</i>	Savanna gardenia	3	4
<b><i>Grewia bicolor</i></b>	<b>Bastard brandy bush</b>	<b>405</b>	<b>966</b>
<b><i>Grewia flava</i></b>	<b>Brandy bush</b>	<b>104</b>	<b>178</b>
<b><i>Grewia flavescens</i></b>	<b>Sandpaper raisin</b>	<b>33</b>	<b>215</b>
<i>Grewia monticola</i>	Silver raisin	26	38

<i>Grewia retinervis</i>		0	1
<i>Grewia</i> spp		0	<1
<i>Lannea discolor</i>	Live-long	1	<1
<i>Maytenus heterophylla</i>	Common spike-thorn	3	106
<i>Maytenus senegalensis</i>	Red spike-thorn	83	9
<i>Maytenus</i> spp		0	3
<i>Ozoroa paniculosa</i>	Common resin tree	3	3
<i>Peltophorum africanum</i>	Weeping wattle	10	16
<i>Pappea capensis</i>	Jacket-plum	68	97
<i>Rhigozum brevispinosum</i>		0	0
<b><i>Rhus leptodictya</i></b>	Mountain karee	144	147
<i>Rhus pyroides</i>		0	9
<i>Rhus</i> spp		0	1
<i>Sclerocarya birrea</i>		2	0
<b><i>Spirostachys africana</i></b>	Tamboti	105	162
<i>Tarchonanthus camphoratus</i>	Wild camphor bush	37	47
<i>Terminalia sericea</i>		0	1
<i>Vitex zeyheri</i>	Silver pipe-stem tree	18	13
<i>Ximenia caffra</i>	Sourplum	4	3
<i>Ximenia americana</i>	Blue sourplum	4	9
<i>Ziziphus mucronata</i>	Buffalo-thorn	7	9
Unidentified		0	30
<b>Total tree/ha</b>		<b>3226</b>	<b>5281</b>

In the follow up study in 2008, eleven new species were recorded that were not found in the baseline study of 1997 (marked grey in table 3). Four species that were recorded in 1997 (marked pink in table 3) were missing in 2007/2008. The three most abundant species, i.e. with the highest density were the same in the baseline study in 1997 as in the evaluation study in 2007/2008. In descending order they were: *Combretum apiculatum*, *Grewia bicolor* and *Dichrostachys cinerea*. The ten species with the highest stem density (marked green in table 3) in 2007/2008 were the three species mentioned above followed by: *Euclea* spp., *Grewia flavescens*, *Grewia flava*, *Acacia tortilis*, *Spirostachys africana*, *Rhus leptodictya* and *Ehretia rigida*.

The stem density had increased from 1997 to 2007/2008 both in the exclosure and control plots (Fig. 2), and there was no statistical difference between the stem densities in the subplots in the different treatments. Thus, the increase in stem density of woody plants does not depend on the treatment.

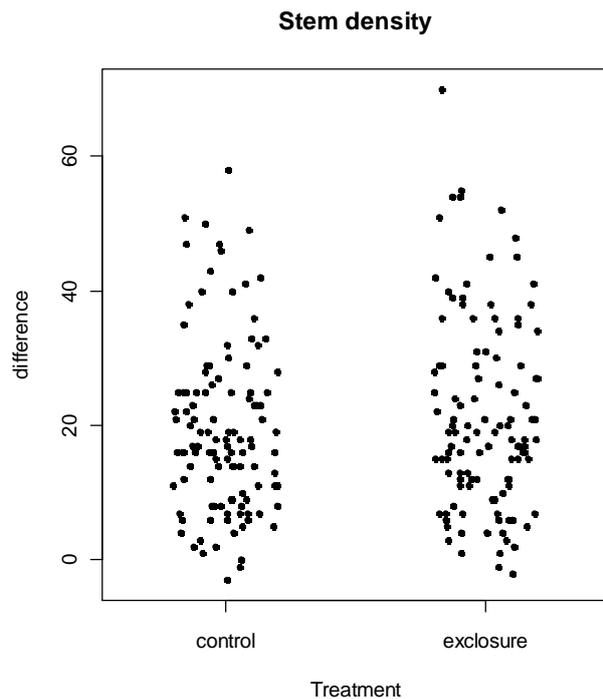


Figure 2. Differences in stem density for each subplot between the baseline study in 1997 and the evaluation study in 2007/2008 for the control and the exclosure treatments.

The difference in stem density in the subplots for the ten most abundant species follows the general trend of increase in density from 1997 to 2007/2008 (Fig. 3) *G. bicolor* shows the largest increase in time but no difference with treatment.

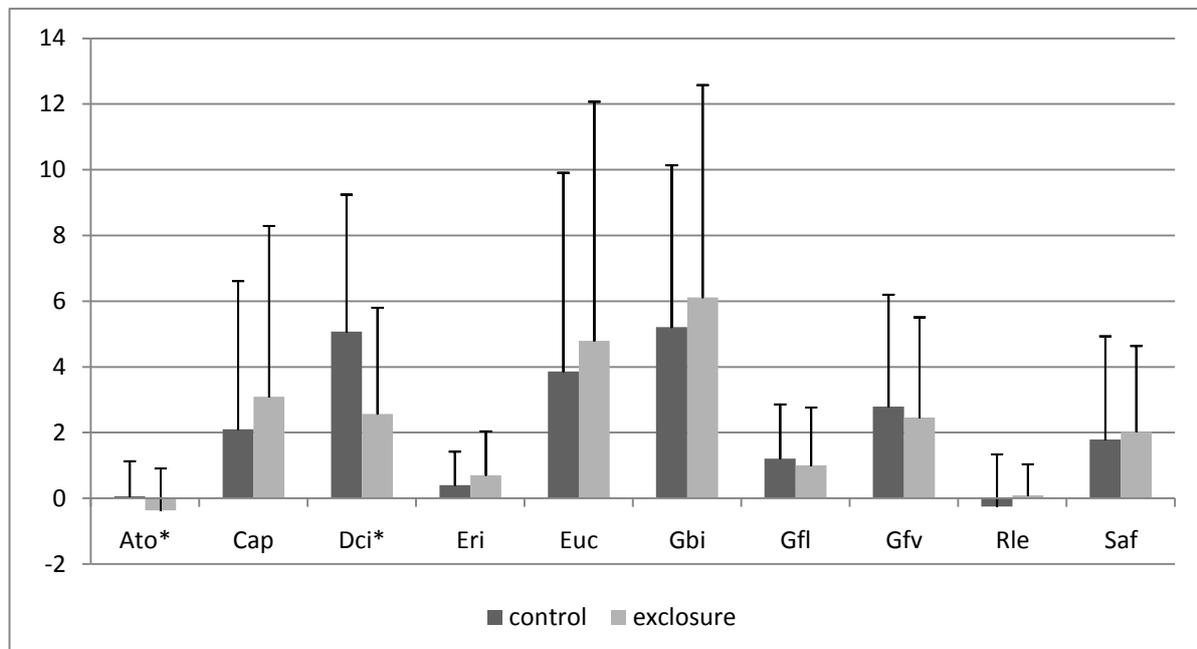


Figure 3. The mean difference in stem density and standard deviation (y-axis) for the subplots, between 1997 and 2007/2008. Significant results are marked with \* (see table 2 for abbreviations).

Only for two of the ten most abundant species there was a significant difference with the treatment (Fig. 3). *D. cinerea* shows a large increase in both exclusion and control (Fig. 4-b), but a significantly larger increase in the browsed control area. Indicating a negative effect of the exclusion of large herbivores ( $p < 0.001$ ) (Bootstrap test). A difference was also shown for *A. tortilis* which increased in the control area and decreased in the exclusion (Fig. 4-a) ( $p = 0.019$ ) (Bootstrap test).

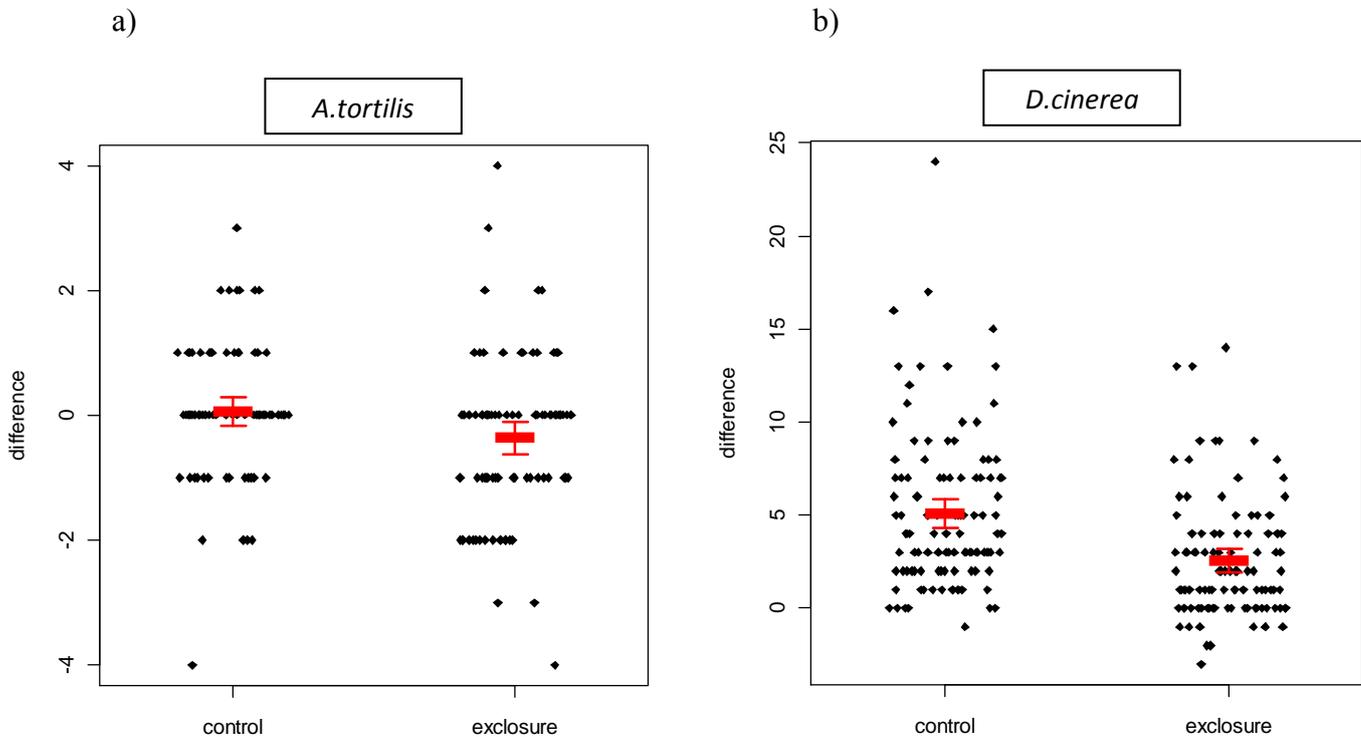


Figure 4 (a-b). Difference in stem density with mean and confidence intervals of a) *A. tortilis* and b) *D. cinerea* in the subplots, in the control and the exclusion treatments.

### Frequency

The frequency is the percentage of subplots in which a species is present. The frequency of the ten most abundant species in the study area did not differ statistically (Fischer's exact test) between treatments or between the baseline study and the evaluation study (Fig. 5). The frequencies of these ten species range from 20 % of the studied subplots up to 100 %. Most of the ten most abundant species show graphically an increase in frequency over time both in the exclusion and the control plots, *G. bicolor* with a frequency of 100 % in the control in the evaluation study in 2007/2008, meaning it was present in all the studied subplots.

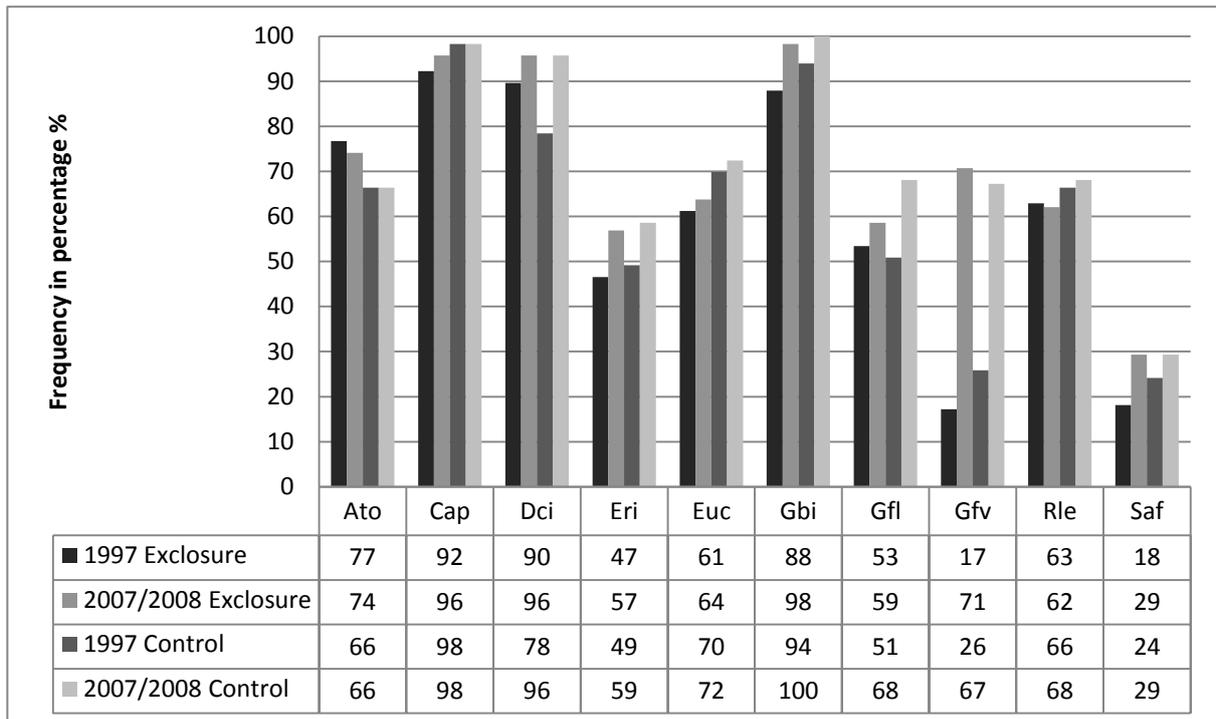


Figure 5. The frequency of the ten most abundant species (abbreviations as in table 2) in the baseline study in 1997 and the evaluation study in 2007/2008.

### Height and Canopy area

Tree height across species increased in the exclosures and decreased in the controls ( $p < 0.001$ ) between 1997 and 2007/2008 (Fig. 6-a). The canopy area shows in general a decrease, but with a significantly larger decrease in the controls than in the exclosures ( $p < 0.001$ ) (Fig. 6-b).

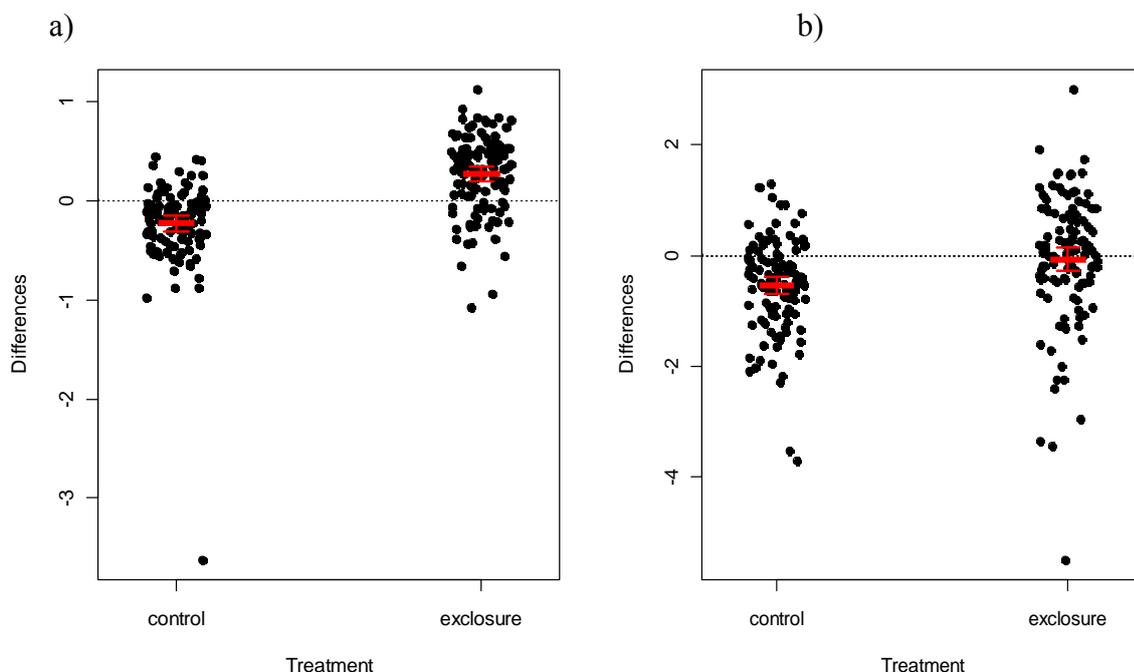


Figure 6 (a-b). The differences in a) mean height and b) mean canopy area in both exclosures and controls, for all trees between 1997 and 2007/2008. Presented in Anova graph with mean and confidence intervals.

There is a positive significant correlation between the tree height and tree canopy area across species for the exclosure and control, both in 1997 and in 2007/2008 (Table 4).

Table 4. Correlation between height and canopy area.

Treatment	Study Year	Correlation Coefficient	p-value (Spearman's)
exclosure	1997	0.68	< 0.0001
exclosure	2008	0.61	< 0.0001
control	1997	0.55	< 0.0001
control	2008	0.61	< 0.0001

The stem density of small ( $\leq 1.0$  m) and large ( $> 1.0$  m) trees has increased over time. In the exclosure the increase of larger trees is significantly higher than in the control ( $p < 0.0001$ ). In the control the smaller trees increased in stem density significantly more than in the exclosure ( $p < 0.001$ ). The differences in stem density can be seen in figure 7 (Fisher's exact test).

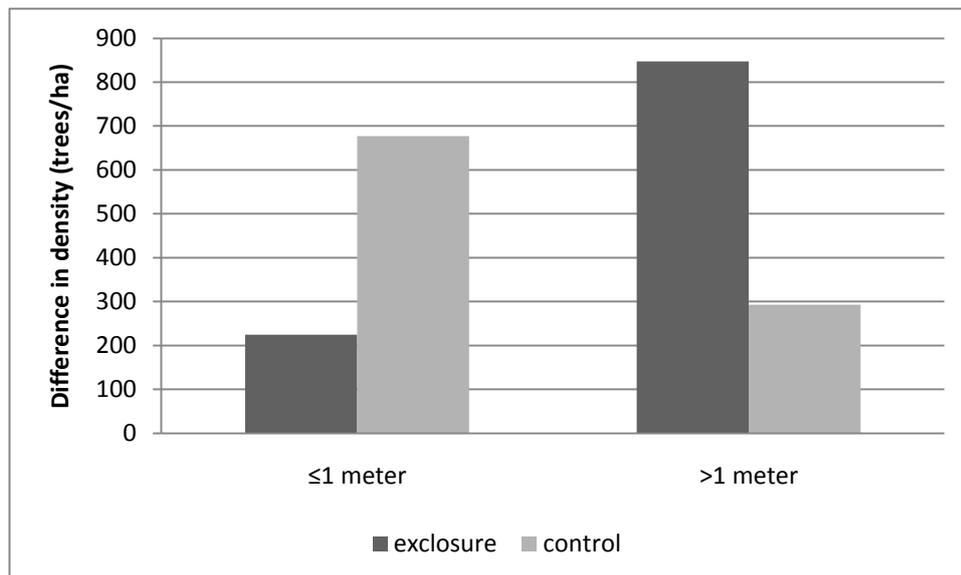
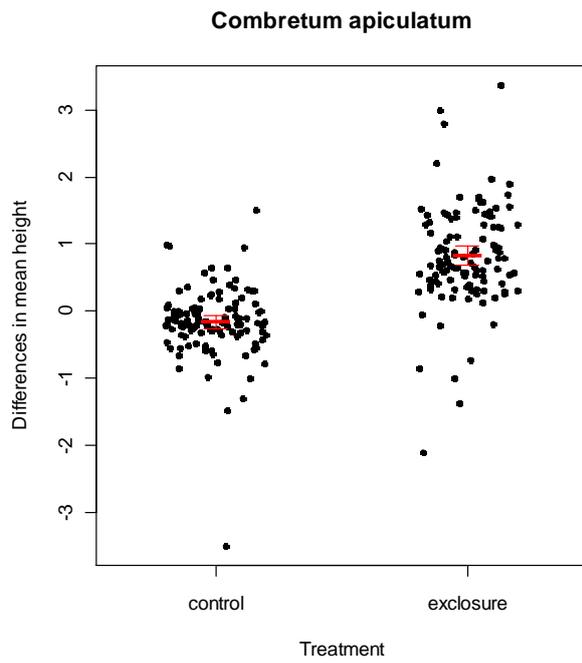


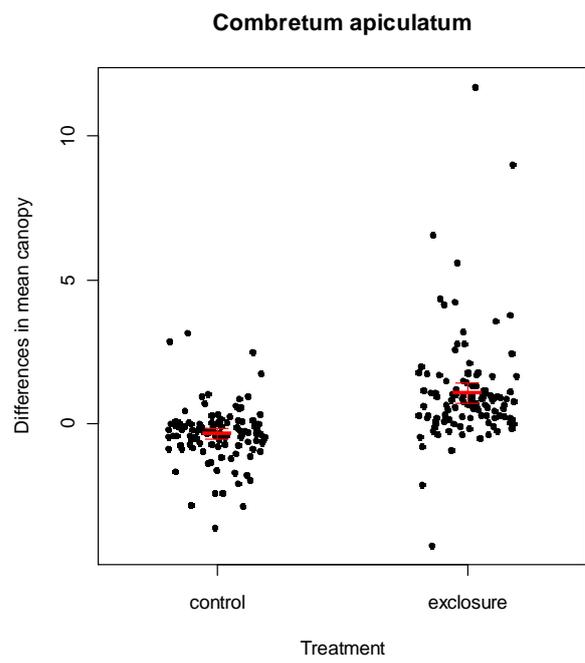
Figure 7. Differences in stem density per hectare between the baseline study in 1997 and the evaluation study of 2007/2008, of trees of 1 m or smaller and of trees taller than 1 m.

An increase in height and canopy area in the exclosures was detected for some of the most abundant species. *E. rigida* had an increase in height (Fig. 8-k), *C. apiculatum*, *D. cinerea*, *G. bicolor*, *G. flavescens* and *R. leptodictya* showed all a significant positive effect of the exclosure treatment for both the height and the canopy area (Fig. 8). *C. apiculatum* (Fig. 8-a), *D. cinerea* (Fig. 8-c), *E. rigida* (Fig. 8-k) and *R. leptodictya* (Fig. 8-i) showed an increase in height in the exclosure subplots while the height of *G. bicolor* (Fig. 8-e) decreased in the control. *G. flavescens* (Fig. 8-g) increased in height both in the control and the exclosure but the increase was much higher in the exclosure subplots. The canopy area of *C. apiculatum* (Fig. 8-b), *D. cinerea* (Fig. 8-d) and *G. flavescens* (Fig. 8-h) increased in the exclosures, while for *R. leptodictya* (Fig. 8-j) it decreased in the controls and increased in the exclosure, and for *G. bicolor* (Fig. 8-f) decreased both in the control and the exclosure but had a larger decrease in the control.

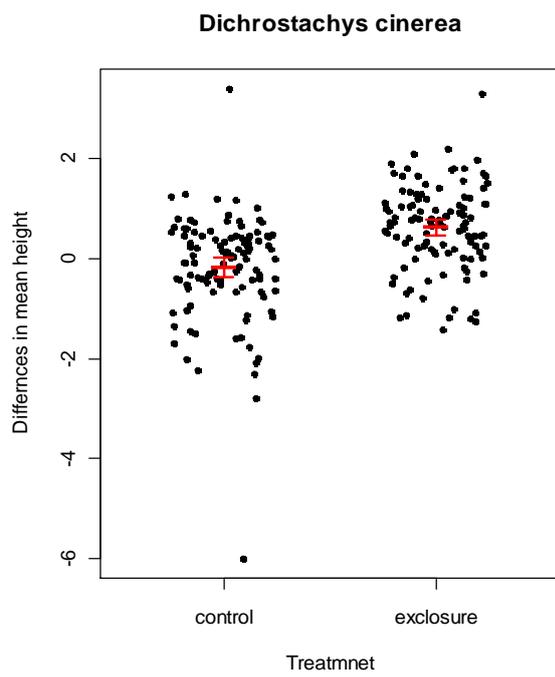
a)



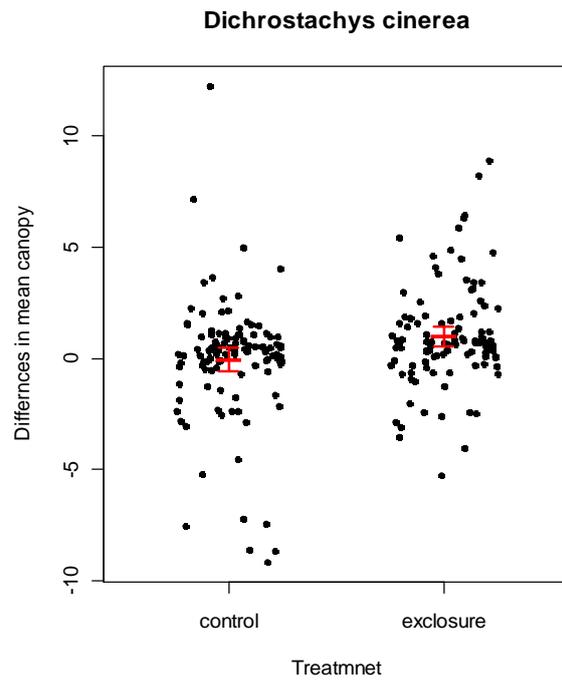
b)



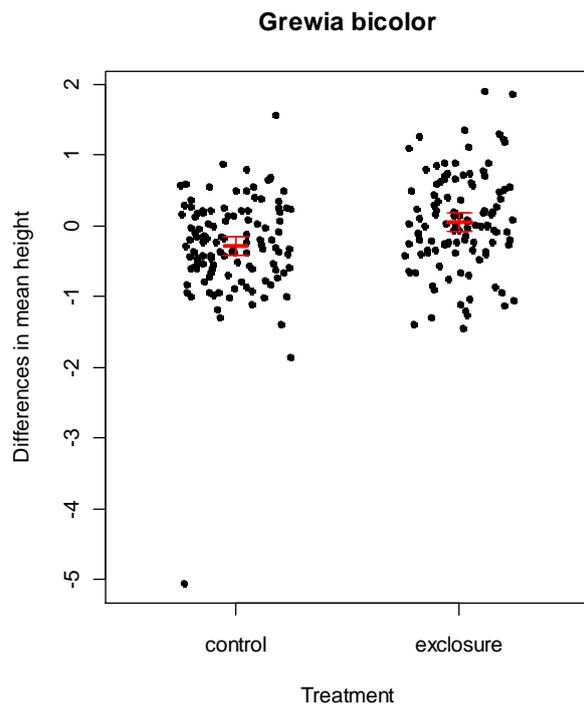
c)



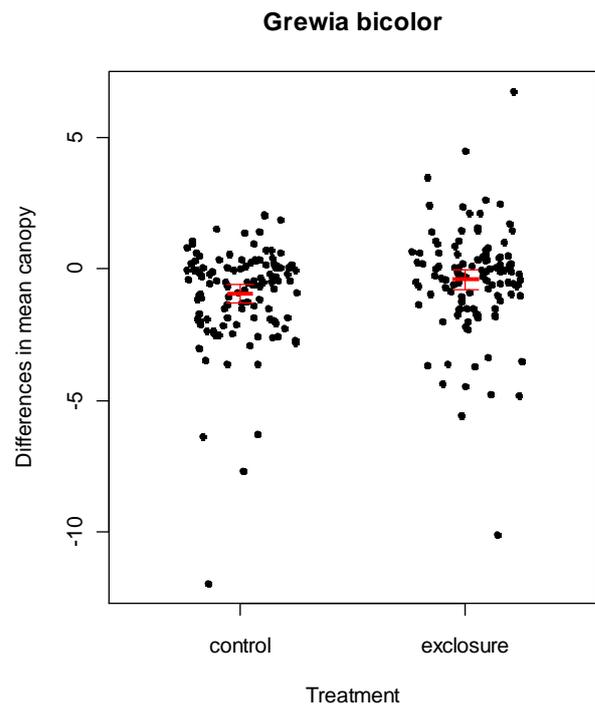
d)



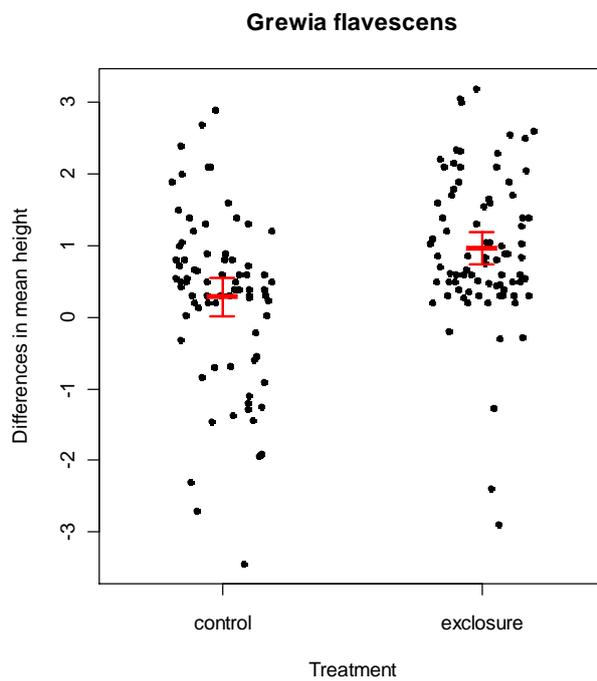
e)



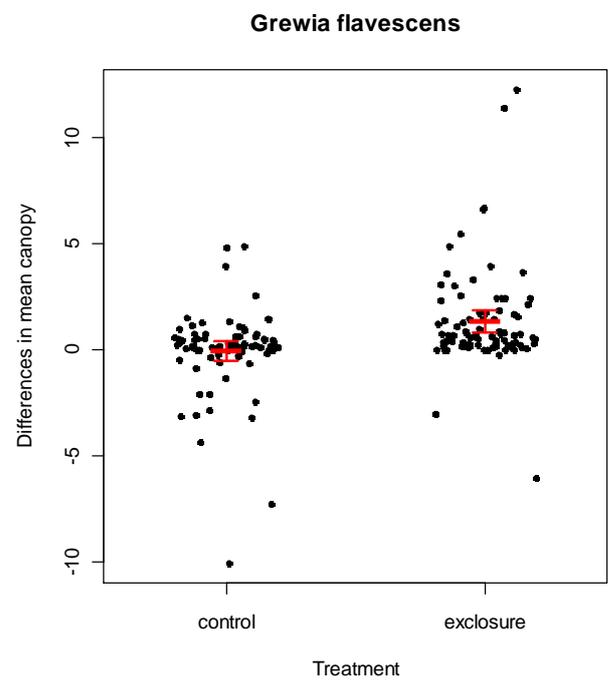
f)



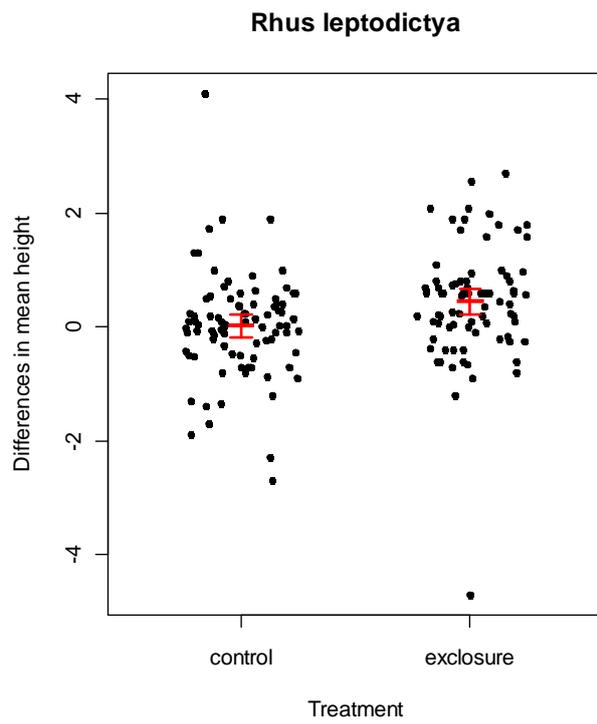
g)



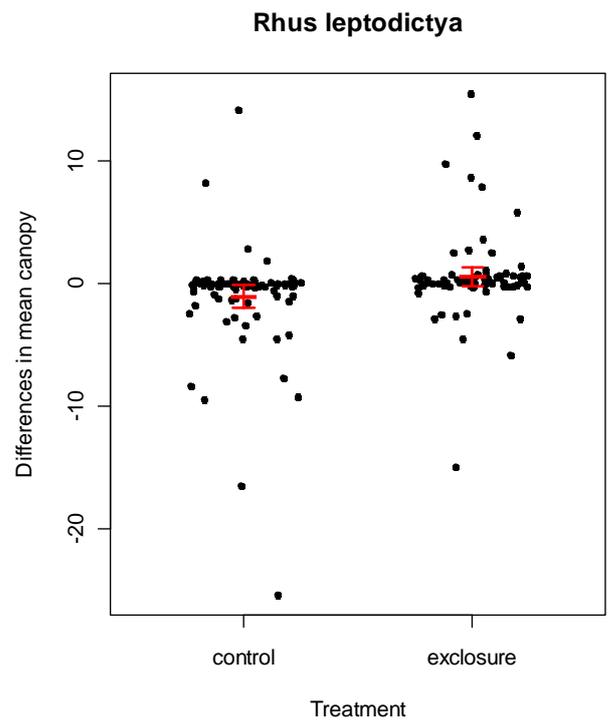
h)



i)



j)



k)

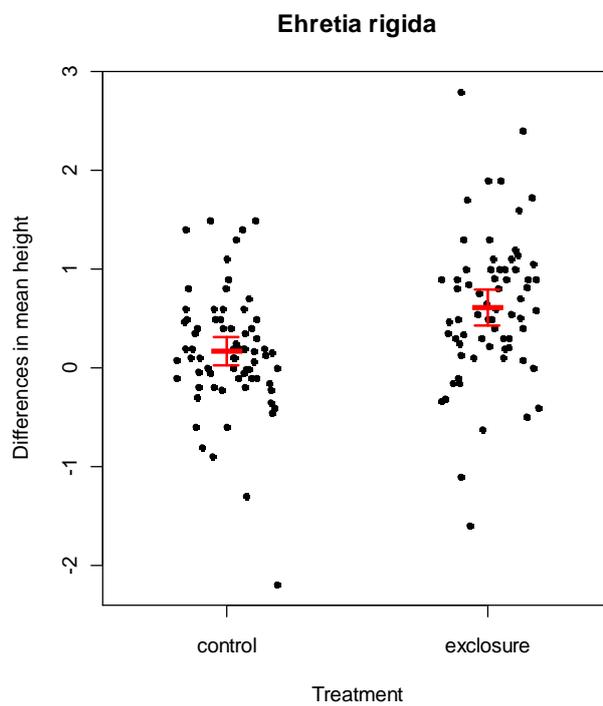


Figure 8 (a-k). The difference in mean height and canopy area with total mean and confidence intervals. Every data point represents a subplot difference between the study of 2007/2008 and the baseline study of 1997. The species in this figure showed all a significant difference.

### Distribution pattern of the trees

The trees in both enclosure and controls show a clear pattern of aggregation both in 1997 and 2007/2008, across species and also for the ten most common species separately. This pattern is shown with the variance to mean ratio. If the variance is larger than the mean the distribution of trees is aggregated and the variance/mean ratio is larger than 1. In table 5 we can see that the trees in the subplots had a larger variance than the mean. The variance/mean ratio seems to increase for most of the species with time.

Table 5. Variance, means and the variance/mean ratio of the number of trees in all the subplots. Separately for 1997 and 2007/2008, and separate for the control and the enclosure of the ten most common species.

Species name		Enclosure		Control	
		1997	2007/2008	1997	2007/2008
<i>Acacia tortilis</i>	Mean	2.04	1.83	1.63	1.60
	s2	4.02	3.32	3.44	2.96
	S2/Mean ratio	1.98	1.81	2.10	1.85
<i>Combretum apiculatum</i>	Mean	10.79	13.56	11.12	13.50
	s2	122.94	217.88	110.83	184.83
	S2/Mean ratio	11.40	16.07	9.96	13.69
<i>Dichrostachys cinerea</i>	Mean	3.19	6.75	2.68	6.34
	s2	10.18	33.14	7.37	28.95
	S2/Mean ratio	3.20	4.91	2.76	4.57
<i>Ehretia rigida</i>	Mean	1.04	1.41	0.81	1.10
	s2	2.62	4.44	2.01	3.20
	S2/Mean ratio	2.52	3.14	2.46	2.90
<i>Euclea spp.</i>	Mean	1.60	4.25	1.57	4.27
	s2	3.54	38.36	3.87	42.21
	S2/Mean ratio	2.21	9.02	2.47	9.87
<i>Grewia bicolor</i>	Mean	4.29	10.34	3.97	9.32
	s2	12.89	64.29	11.59	58.12
	S2/Mean ratio	3.01	6.22	2.92	6.24
<i>Grewia flava</i>	Mean	1.09	1.78	0.86	1.61
	s2	2.58	5.23	1.52	4.24
	S2/Mean ratio	2.37	2.94	1.77	2.63
<i>Grewia flavescens</i>	Mean	0.35	2.25	0.38	2.08
	s2	0.81	12.68	0.82	11.99
	S2/Mean ratio	2.31	5.63	2.17	5.76
<i>Rhus leptodictya</i>	Mean	1.70	1.63	1.54	1.46
	s2	3.82	3.92	3.56	3.46
	S2/Mean ratio	2.25	2.40	2.31	2.37
<i>Spirostachys africana</i>	Mean	1.10	1.76	0.86	1.37
	s2	9.80	19.51	7.47	14.59
	S2/Mean ratio	8.92	11.11	8.73	10.66

## Correlations

Spatial correlations of the stem density between the ten most abundant species were found between some of the species (Table 6). Most of the statistically significant correlations that were found shifted in time and with treatment, showing no real pattern. Four of the correlations were found to be constant in time, both in the exclosure and the control; it was *C. apiculatum* having a significant negative correlation to *A. tortilis*, *D. cinerea*, *E. rigida* and *G. bicolor* ( $p < 0.05$ , Spearman's correlation).

Table 6. The correlation coefficient between the stem densities of trees for *C. apiculatum* correlated to *A. tortilis*, *D. cinerea*, *E. rigida* and *G. bicolor*.

Correlations	<i>C. apiculatum</i>			
	Exclosure		Control	
	1997	2007/2008	1997	2007/2008
<i>A. tortilis</i>	-0.37	-0.30	-0.34	-0.29
<i>D. cinerea</i>	-0.34	-0.34	-0.38	-0.36
<i>E. rigida</i>	-0.35	-0.35	-0.26	-0.15
<i>G. bicolor</i>	-0.43	-0.39	-0.43	-0.34

## Discussion

### Abundance

The result clearly showed a strong trend of increasing density of trees from the baseline study to the evaluation study, with an increase of 63 %. Since the density of trees increased in the same way both in the control and exclosure subplots, we can conclude that this increase is not due to the treatment of excluding large herbivores from the study plots. The increase in trees in the area could be because the area is still recovering from the exclusion of cattle since 1986, when the reserve was fenced to keep the cattle out and only allowed the introduced wild animals to browse. Grazing by cattle has a more pronounced effect on the vegetation than grazing by wild large herbivores (Goheen *et al.* 2010). When trees increase in stem density it may change the tree/grass ratio, suppressing grasses and herbs. This leads to the so called bush encroachment, but the driving factors behind this are not yet well understood (Ward 2005). It is usually believed that it is caused by heavy grazing, but several studies have shown that the causes are more complex than that (Scholes & Archer 1997, Silva *et al.* 2001). In this case the grazing pressure has decreased without the cattle. Since there was no difference between treatments the browsing and grazing by wild large herbivores alone has not caused a bush encroachment during the time span studied. Due to the experimental design I cannot separate between the effects of browsers, intermediate feeders and grazers, but considering the high population densities of the browsers and their direct impact on the woody plants, I assume the effect of the browsers being considerably higher on woody vegetation if compared to grazers

The Mokolodi nature reserve had a policy to put out all the fires in the reserve, this may also have protected the vegetation from not only cattle but fire, one of the main determinants for the dynamics of the savanna ecosystem (Frost *et al.* 1986). The absence of fire may have had some effect on the increase in stem density in the study area, since fire has been suggested to play a major role in suppressing the increase in woody vegetation (Roques *et al.* 2001). But several results indicate that fire alone is not determining the density of trees in the savanna but interacts with grazing and browsing pressure, water and nutrient availability and land use (Silva *et al.* 2001). Grazers, browsers and fire all interact in determining the grass to tree ratio. Grazing reduces the fuel for the fires which leads to less intense fires which in turn increase woody plants. Browsers reduce the woody plants and

facilitate the growth of grasses which then lead to more intense fires (Fulbright *et al.* 2010). The effects of the absence of fire cannot be ruled out in this study. And fire can then be a factor for the increase of stem density that has been recorded in the study area both with and without large herbivores. Fires are believed to cause decrease in woody vegetation, while browsers inhibit the recovery of the woody vegetation (van Langevelde *et al.* 2003). Another determinant for the vegetation structure is soil resources which may play a role for my results but was not included in this study. Soil conditions have been shown to strongly interact with herbivory on its influence on the plant communities (Aarrestad *et al.* 2011).

New species appeared in the studied subplots in 2007/2008 that were not in the respective subplots in the baseline study of 1997. This could mean that new species have found their way to the study area. Also there were a few species recorded in 1997 that were missing in the study of 2007/2008. Since the density of these species is low it means they could still be present in the area, but not in the studied subplots. The three species that disappeared could also be included among the unknown species, since we found 70 trees that we were not able to successfully identify. *Acacia fleckii* was only found in the study in 2007, and I think this could be due to a misidentification, confused with *Acacia erubescens* because of their similarity, but the presence of this species cannot be ruled out.

For all the species together the treatment of excluding large herbivores did not have an effect on the stem density and neither for eight of the ten most abundant species separately. But since changes in vegetation usually have a slow response or have no response to a termination of browsing (Husheer *et al.* 2003), the composition of the vegetation may need more time to start showing any clear changes. So therefore I cannot reject my hypothesis that larger herbivores have an effect on stem density.

One of the two species that the treatment had an effect on was *D. cinerea* which had an increase in both enclosure and control, but had a significantly larger increase in the control than in the enclosure. These results indicate a negative effect from the exclusion of large herbivores. This species grows better in the control where large herbivores are still present, and therefore benefits from the disturbance that the browsing causes. This could be due to that *D. cinerea* is a stronger competitor for resources when the vegetation is disturbed by browsing. *D. cinerea* was also one of the most browsed species and is a species known to colonize disturbed areas. And even though it is browsed mostly during dry seasons, it is known as a fast growing species and therefore grows well in browsed areas. *A. tortilis* was also affected by the treatment, showing that it grows better in the controls where the browsing is still present. In the enclosure where the browsing is terminated, it has decreased in stem density. In a previous study Dharani *et al.* (2008) showed that browsing can reduce height and canopy area rather than stem density, and instead even activate seedling regeneration. This could explain my study's results where *A. tortilis* had a reduced stem density in the enclosure where the browsing had been terminated. Similar studies have also shown that *A. tortilis* do not regenerate as well in protected areas. Due to that browsing may cause disturbance as for example trampling of the soil, which facilitates the water infiltration into the ground. The absence of this may inhibit seed germination (Nuomi *et al.* 2010). Both *D. cinerea* and *A. tortilis* are woody plants that tolerate browsing. They grow better in the area where there is continued browsing pressure, and this could indicate a shift in the ecosystem dominated by less browsing tolerant species.

### **Height and Canopy area**

I expected the trees to grow higher and with a wider canopy area in the enclosure, where the trees are protected from large herbivores. This agrees with our visual observation that the enclosures looked denser. Browsing can reduce woody vegetation by reducing the size of the trees (van Langevelde 2003). Therefore in this study the trees across species grew higher and with a wider canopy area as expected. This result could be because the small trees can grow taller when they are

protected, and it has indeed been shown that young trees grow more rapidly when they are protected from herbivory (Frost *et al.* 1986).

The result showed that trees grew higher and with a wider canopy, this could mean either that there are more tall trees in the enclosure, or that there are more seedlings or smaller trees in the control. Some of the subplots showed an increase and others a decrease in average height and canopy area. But this results could be due to that it only looks at the average tree height of a subplot, and the average is sensitive to extreme values, like for example if a subplot has many trees below 1.0 m, it will have a major effect on the average. This could mean that there are more small trees in the control taking the average down. When the trees were divided in two groups, small and larger ones, a highly significant difference between the treatments appeared: small trees ( $\leq 1.0$  m) had increased significantly in the control and the larger trees ( $> 1.0$  m) had increased significantly in the enclosure. There might be larger trees in the enclosure because they can grow freely without being browsed, so the resources that go to recover from browsing can instead be used for growing higher. The lack of small trees can be because there are not enough of openings in the canopy area giving space for seedlings to establish. Also the large herbivores can have a positive effect on seedling survival by suppressing the negative effects on seedlings by small herbivore pressure of insects and rodents which were not included in this study (Goheen *et al.* 2004). The increase in numbers of small trees in the control can be because they stay small for a longer period, as a result of being browsed, since repeated browsing prevents the trees from growing into larger size classes to escape the herbivore feeding height (Nyengera & Sebata 2009). Browsed trees could either grow taller than unbrowsed ones to escape the browsers' height limitation to feed, or they could grow smaller as a result of relocation of the resources after tissue loss to other use than height growth (Côte *et al.* 2002). In this case the browsed trees are smaller; not only on average, but also the stem density of small trees was higher in the control plots than in the enclosures.

There was a positive reaction in six of the ten most abundant species in height growth and in five species in their canopy area by the exclusion of larger herbivores. This could indicate differences in how tolerant the different species are (Côte *et al.* 2002). These species may not tolerate browsing well and grow better with the exclusions of large herbivores, or are better competitors for resources when the herbivore pressure is relieved.

*C. apiculatum* grew significantly higher in the enclosure where the browsing of large herbivores had been terminated, and it also had a larger canopy area there. Similar results were found in a previous study at Mokolodi Nature Reserve where leaf browsing on *C. apiculatum* was simulated, resulting in reduced height growth in trees (Rooke & Bergström 2007).

### **Distribution pattern of the vegetation**

As expected all the studied species showed an aggregated spatial distribution. For plant spatial distribution there is three different patterns: random, regular or aggregated. Here we expected the most common one, which is the aggregated pattern, meaning that the neighboring individuals of the same species form groups or clumps. While in random distribution each individual of a species is independent of the other individuals (Gurevich 2002). This aggregation was found both at the baseline study and the evaluation study. A larger mean to variance ratio is shown in the results, which could mean that the aggregation is larger in the evaluation study than in the baseline study. It has been found that aggregated populations are very common, and two causes have been suggested for this. One of the causes behind this could be that even if seeds may fall at random the habitat may not be homogenous, and therefore the proportion of germinating seeds may vary between areas, causing seeds to form groups or clumps. But also if the habitat is homogenous the individual plants may occur in groups or clumps if they reproduce vegetatively or with seeds that have small dispersal ability (Pielou 1960).

Some of the ten most abundant species were spatially correlated to each other: *C. apiculatum* was negatively correlated to four other species, *A. tortilis*, *D. cinerea*, *E. rigida* and *G. bicolor*. These correlations were found in the enclosure and the control plots, both in the baseline study and in the evaluation study. This showed that *C. apiculatum* does not grow well together with these other species. *C. apiculatum* is already the species with the highest stem density has a high frequency and grows aggregated. It seems to be more effective in the competition with its neighbors. This species may also have different soil preferences for growing and therefore also grows in different vegetation zones. The study area consisted of the acacia vegetation zone where *A. tortilis* is one of the dominant species. Another vegetation zone in the nature reserve is the combretum zone dominated by *C. apiculatum*. This could be indicating a change of vegetation zone, where *C. apiculatum* dominates instead of *A. tortilis* which is a species with an abundance which has not increased, in contrast to the other species and in contrast to the general trend of increased stem density across species.

## **Conclusions**

There was no effect in density of the treatment of excluding large herbivores for 10-11 years in this study across all species. But a clear increase in stem density was showed for the area, which indicates increased woody vegetation. This is today a common phenomenon in semi-arid regions of the world, and therefore demands more future studies for a better understanding of its causes. Also there are other factors not included in this study that may play an important role in understanding the changes in vegetation structure, such as fire, soil and nutrients which should be included in future studies. Looking at specific species the time span of 10-11 years was enough to show that *A. tortilis* and *D. cinerea* are species that benefit from the browsing by large herbivores. In a longer time perspective more species may show some effects of exclusion of large herbivores as well. This study also showed that even if the stem density did not change with the exclusion of large herbivores across all species, the height and the canopy area was negatively affected by browsing pressure.

## **Acknowledgments**

I would specially like to thank my supervisors Christina Skarpe, Roger Bergström and Ingvar Backéus for all the supervising and comments on my written work during this period. I would also like to thank Moffat Setshogo for the help with the species identification during the fieldwork. I want to thank the Committee of Tropical Ecology (ATE) for admitting this project as a Minor field study and thanks to the Swedish International Development Authority (Sida) for funding it. I also acknowledge the Ministry of Environment, Wildlife and Tourism for the research permit in Botswana. And thanks to Mokolodi Wildlife Foundation for the accommodation, and for the opportunity to walk around in this amazing reserve to carry out the field work at the Mokolodi Nature Reserve. I want to give a big thanks to Hanna Leife for a great partnership during the field work in Botswana and for the support during the writing of the thesis, I am also very grateful to Thsegofatso Gideon and Mooketsi “General” Richard for a great field assistance which allowed us to collect a large amount of data. Thank you also to Didrik Vanhoenacker for being a great teacher and leading the best course in statistics which taught me how to perform all the statistics in this thesis. I would also like to give a big thanks to Karolina Norrman for being a great supporting friend during all this time! And final a big thank to my mother for being who she is!

## References

- Adler, P.B., Raff, D.A., Lauenroth, W.K. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465-479
- Aarrestad, P.A., Masunga, G.S., Hytteborn, H., Pitlagano, M.L., Marokane, W., Skarpe, C. 2011. Influence of soil, tree cover and large herbivores on field layer vegetation along a savanna landscape gradient in northern Botswana. *Journal of Arid Environments* 75: 290-297
- Baraza, E., Zamora, R., Hódar, J. A. 2006. Conditional outcomes in plant-herbivore interactions: neighbors matter. *Oikos* 113: 148-156
- Bergström, R. 1992. Browse characteristics and impact of browsing on trees and shrubs in African savannas. *Journal of Vegetation Science* 3: 315-324
- Bergvall, U.A., Rautio, P., Sirén, H., Tuomi, J., Leimar, O. 2008. The effect of spatial scale on plant associational defenses against mammalian herbivores. *Ecoscience* 15: 343-348
- Bilbrough, C. J. and Richards, J. H. 1993. Growth of sagebrush and bitterbrush following simulated winter browsing: mechanisms of tolerance. *Ecology* 74: 481-492
- Coates-Palgrave, M. 2002. *Trees of Southern Africa* 3<sup>rd</sup> edn., 2<sup>nd</sup> imp. Struik Publishers, Cape Town
- Cooper, S.M., Owen-Smith, N., Bryant, J.P. 1988. Foliage acceptability to browsing ruminants in relation to seasonal changes in the leaf chemistry of woody plants in a South African savanna. *Oecologia* 75: 336-342
- Côte, S.D., Rooney, T.P., Tremblay, J-P, Dussault, C., Waller, D.M, 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics* 35: 113-47
- De Knegt, H. J., Groen, T. A. 2008. Herbivores as architects of savannas: including and modifying spatial vegetation patterning. *Oikos* 117: 543-554
- Dharani, N., Kinyamario, J.I., Wagacha, P.W., Rodriguez, A.J. 2008. Browsing impact of large herbivores on *Acacia xanthophloea* benth in lake Nakuru national park, Kenya. *African Journal of Ecology* 47: 184-191
- Edenius, L., Bergman, M., Ericsson, G., Danell, K., 2002. The role of moose as a disturbance factor in managed boreal forests. *Silva Fennica* 36: 57-67
- Frost, E., Medina, E., Menaut, J-C., Solbrig, O., Swift, M. and Walker, B. 1986. Responses of savannas to stress and disturbance. *Biology International, special issue* 10: 1-82
- Fulbright, T.E., Dacy, E.C., Drawe D. L. 2011. Does browsing reduce shrub survival and vigor following summer fires? *Acta Oecologica* 37: 10-15
- Goheen, J.R., Keesing, F., Allan, B.F., Ogada, D., Ostfield, R.S. 2004. Net effects of large mammals on *Acacia* seedling survival in an African savanna. *Ecology* 6: 1555-1561

- Goheen, J.R., Palmer, T.M., Keesing, F., Riginos, C., Young, T.P. 2010. Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. *Journal of Animal Ecology* 79: 372-382
- Greig-Smith, P. 1983. *Quantitative Plant Ecology*, 3<sup>rd</sup> edn., 9<sup>th</sup> Vol. University of California Press. Page 62.
- Gurevich J., Scheiner S.M., Fox G.A., 2002. *The ecology of plants*. First edition. Sinauer Associates
- Hester, A.J., Edenius, L., Buttenschon, R.M., Kuiters, A.T. 2000. Interactions between forests and herbivores: the role of controlled grazing experiments. *Forestry* 73: 381-9
- Hjältén, J., Danell, K. and Lundberg, P. 1993. Herbivore avoidance by association: vole and hare utilization of woody plants. *Oikos* 68: 125-131
- Hjältén, J. and Price, P. W. 1997. Can plants gain protection from herbivory by association with unpalatable neighbors? A field experiment in a willow-sawfly system. *Oikos* 78: 317-322
- Husheer, S.W., Coomes ,D.A., Robertson, A.W. 2003. Long-term influences of introduced deer on the composition and structure of New Zealand *Nothofagus* forests. *Forest Ecology and Management*. 181: 99-117
- Jeltsch, F., Milton, S.J., Dean, W.R.J., Van Rooyen, N. 1996. Tree spacing and coexistence in semiarid savannas. *Journal of Ecology* 84: 583-595
- Kingdon, J. 2004. *The kingdon field guide to African mammals*. 1997. Academic Press
- Noumi, Z., Touzard, B., Michalet, R., Chaieb, M. 2010. The effects of browsing on the structure of *Acacia tortilis* (Forssk.) Hayne ssp. *raddiana* (Savi) Brenan along a gradient of water availability in arid zones of Tunisia. *Journal of Arid Environments* 74: 625-631
- Nyengera, R. and Sebata, A. 2009. Effect of eland density and foraging on *Combretum apiculatum* physiognomy in a semi-arid savannah. *African Journal of Ecology*. 48: 45-5
- Pielou, E.C, 1960. A single mechanism to account for regular, random and aggregated populations. *Journal of Ecology* 48: 575-584
- Rooke, T. 2003. *Defences and responses: woody species and large herbivores in African savannas*. Doctoral thesis, Department of Animal Ecology, Swedish University of Agricultural Sciences
- Rooke, T. and Bergström, R. 2007. Growth, chemical responses and herbivory after simulated leaf browsing in *Combretum apiculatum*. *Plant Ecology* 189: 201-212
- Roques, K.G., O'Connor, T.G., Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* 38: 268-280
- Scholes, R.J and Archer, S.R. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28: 517-544

- Silva, J.F., Zambrano, A., Fariñas, M.R. 2001. Increase in the woody component of seasonal savannas under different fire regimes in Calabozo, Venezuela. *Journal of Biogeography* 28: 977-983
- Skarpe, C. 1992. Dynamics of savanna ecosystems. *Journal of Vegetation Science* 3: 293-300
- Skarpe, C., Bergström, R., Bråten, A.L. and Danell, K. 2000. Browsing in a heterogeneous savanna. *Ecography* 23: 632-640
- van Langevelde, F., van de Vijver, C.A.D.M., Kumar, L., van de Koppel, J., de Ridder, N., van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J, Prins, H.H.T., Rietkerk, M. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84: 337-350
- Van Wyk, B., Van Wyck, P. 1997. *Field guide to trees of southern Africa*. 1997. Struik Pub
- Ward, D., 2005. Do we understand the causes of bush encroachment in African savannas? *African Journal of Range and Forage Science* 22: 101-105
- Wiegand, K., Ward, D., Saltz, D. 2005. Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer. *Journal of Vegetation Science* 16: 311-320