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Has woody vegetation in a semi-arid savanna changed after 11 years exclusion of large herbivores?



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Abstract

Large herbivores are seen as ecological determinants of African savannas because of the effects that browsing and grazing have on the savanna ecosystem. The selective feeding by browsers on woody plants is believed to play an important role for development of shrub and tree layers. It is also generally acknowledged that herbivory has led to a number of plant responses to protect the plant resources which can be seen as adaptations to predation. Plant adaptations to resist herbivory are often divided in avoidance and tolerance strategies. Physical defence is one of the avoidance strategies and in arid and semi-arid savannas physical defence like spines, hooks and thorns is particularly frequent. Previous studies have shown evidence that these kinds of defence are inducible and facultative. I studied the impact of excluding large browsing herbivores from a semi-arid savanna in southern Botswana. I focused on differences between browsed areas and 11 year-old unbrowsed exclosures in density of trees, species composition and density of spinescent trees. I also looked into differences in length and density of spines within three species. I did not find any significant differences in change in density of trees, species composition or proportion of spinescent trees between browsed and non browsed areas. Neither did I find any differences in spinescence within the three species that I studied in the browsed and non-browsed areas. The study did, however, reveal an overall increase in tree density since 1997.

Key words

Botswana, browsing, spinescence, exclosure, vegetation dynamics

Introduction

Savannas are tropical or near-tropical seasonal ecosystems with a continuous herbaceous layer, usually dominated by grasses, and a discontinuous layer of trees and/or shrubs (Frost *et al.* 1986). Savannas cover approximately 20% of the world's land surface, and about 50% of Africa (Scholes and Walker 1993). They support a large proportion of the world's human population and most of its livestock and wild herbivore biomass (Scholes and Archer 1997). Herbivory includes browsing and grazing and because of the different impacts grazing and browsing have on the vegetation (van Langevelde *et al.* 2003) herbivory may affect not just the abundance and distribution of the forage species, but also the dynamic balance between grasses, trees and shrubs and therefore all the structure and function of the savanna ecosystem. Large herbivores have therefore for long been seen as ecological determinants of African savannas together with soil nutrients, water and fire (Scholes and Walker 1993).

Tree density

Large herbivores seem also to play a role in reducing nutrient leakage from the surface-soil in savanna grasslands (Ruess 1987), indicating that the extinction or even exclusion of large herbivores from savanna grasslands may lead to an increase in woody growth, as nutrients leak to deeper soil layers (Hatton and Smart 1984). Increases in the cover of woody vegetation in savannas have been reported from many arid and semi-arid parts of the world. So called bush encroachment has been attributed to human disturbance, primarily overgrazing by livestock (Skarpe 1990b). Nowadays many scientists believe that the processes behind bush encroachment are more complex than heavy grazing (Ward 2006, Britz and Ward 2007, Scholes and Archer 1997).

Woody cover increase will, however, lead to competition for resources not only between grass and woody species but among trees as well. Tree-tree interactions are the ones likely determining density and pattern of woody plant distribution (Scholes and Archer 1997). Plants can only grow in size until the limiting resource, in this semi-arid savanna presumably moisture (Skarpe 1990a), is fully utilized. Thereafter any increase in plant size will lead to competition for resources within plant populations with subsequent decrease in plant density (Guo *et al.* 1998). This kind of density-dependent mortality due to competition for resources within the population, is called self-thinning (Westoby 1984). The expectation is therefore a higher increase in tree density in areas with initial low tree density compared to areas with already high tree density when resources are limited. But intraspecific competition is not the only factor that can lead to mortality, other disturbance and stress factors like for example interspecific competition and herbivory can as well (Guo *et al.* 1998).

Species composition

Large browsers, herbivores feeding on woody plants or herbaceous dicots (Shipley 1999), feed selectively and may affect plants directly, mainly through consumption. Selective feeding, i.e. disproportionate consumption of certain woody species, individuals or plant parts is believed to be of great importance for the development of shrub and tree layers (Pastor and Naiman 1992). The result of selective feeding on species level is that individuals of palatable species are consumed and sensitive ones may lose competitive power and will be outcompeted, while less palatable species and more tolerant palatable species may increase at their expense (Gill 2006).

Functional trait: spinescence and intraspecific differences

Although selectivity by browsers for woody plants is not well understood, a number of morphological and chemical traits in plants, such as fast growth, high nutrient concentration and low concentration of chemical defences, can be related to preference by herbivores.

However, many nutrients that are essential for herbivores are also essential for the plants themselves, and it is recognized that herbivory has led to the evolution of plant responses to protect the resources, which can be seen as adaptations to predation, such as the development of morphological structures like thorns and hairs (van Wieren and Bakker 2008). The degree to which defences are expressed can vary between populations or between individual plants within a species and in the same plant over time depending on, e.g., size, phenology or previous browsing (Skarpe *et al.* 2000).

Plant resistance strategies to herbivory are divided into avoidance strategies and tolerance strategies (Rosenthal and Kotanen 1994), and expressed as functional traits. The classification of plants with similar combinations of traits in functional types is based on plants' function instead of their taxonomic identity (Cornelissen *et al.* 2003) The plants' functional type influence which plants will be most competitive and dominating in vegetation with and without herbivory under different resource availability. Species with certain traits will be hit hard even by a low browsing pressure, while other species are avoided or tolerant for herbivory and may even benefit from herbivory-induced reduction in interspecific competition (Gill 2006). While tolerance for herbivory often is developed by plants evolved in resource rich environments plants evolved in resource poor environments tend to have avoidance traits (Skarpe and Hester 2008). Avoidance can either be escape (e.g. growing high to avoid being browsed, growing inside defended species or growing flat on the ground) or chemical and physical defence (Hester *et al.* 2006). Physical defence, like hairs, hooks and thorns, are hypothesised to have evolved as a defence against foraging by large herbivores (Bazely *et al.* 1991, van Wieren and Bakker 2008). Spinescence does not actually prevent browsing, but it may reduce plant losses to large herbivores (Skarpe and Hester 2008), because it slows down the rate of feeding and reduces bite size on shoots (Gill 2006, Skarpe *et al.* 2000). Browsing pressure has been shown by Skarpe *et al.* (2000) in a southern African savanna to be 2.5 times higher on species without spines than on spinescent ones. Even within a species herbivores prefer individuals that are less spinescent (Bazely *et al.* 1991, Obeso 1997). Long straight spines have been shown to be more efficient in reducing twig biting, while small hooks protect against leaf stripping (Skarpe *et al.* 2000). This kind of physical avoidance mechanism is particularly frequent in arid and semi-arid shrub lands and previous studies have shown strong evidence that the degree of expression, e.g. density or size of spines may be inducible or facultative (Hester *et al.* 2006, van Wieren and Bakker 2008, Young *et al.* 2003, Bazely *et al.* 1991). The theory for induced plant defence predicts that defence will occur when benefits exceed the costs (Scholes and Walker 1993).

Thus, herbivores directly affect the woody layer in terms of species composition and/or abundance of the various species which in turn may have far-reaching consequences for the savanna ecosystems with many direct impacts and a multitude of indirect or cascading effects on all trophic levels (Hester *et al.* 2006, Ward 2006, Gill 2006, Hobbs 2006, Pastor *et al.* 2006, Weisberg *et al.* 2006). As the population densities of wild large herbivores have changed (mostly decreased) considerably in many African savannas, not least as a result of human-related activities (du Toit and Cumming 1999), and particularly African savannas are believed to owe their existence more to the impact of large herbivores and fire than to climate (Skarpe 1992), it is most relevant to increase our knowledge on large herbivore impact on savanna ecosystems. One way of doing that is to use fences to exclude large herbivores and compare the vegetation development in the exclosures with that in grazed/browsed unfenced areas.

Aims and hypotheses

This project focuses on the impact of excluding large herbivores in a semi-arid savanna ecosystem in south-eastern Botswana with special focus on density of trees, species composition and proportion of spinescent trees, in relation to browsing pressure. I compare changes in the total tree density, and changes in tree density in areas with initial low and high densities. I also look into species frequency of woody plants as well as differences in proportion of trees with or without spines, hooks and thorns between grazed/browsed areas and areas that have been protected from herbivores for 11 years. Finally I examine changes of spinescence within three species.

The aim was to test the hypotheses that

- the density of trees is higher in areas without large herbivores than in areas with large herbivores,
 - and even higher in areas with initially low tree density than in areas with initially high tree density.
- species that are selected for by herbivores are more abundant in areas not exposed to browsing than in browsed areas.
- spinescent species (with spines, hooks or thorns) are more abundant in areas exposed to browsing than in unbrowsed areas.
- spinescent plants that are exposed to browsing have a higher density of spines, hooks or thorns compared to plants of the same species that are protected from browsers.
- spinescent plants that are exposed to browsing have longer spines, hooks or thorns compared to plants of the same species that are protected from browsers.

Methods

Study area

The fieldwork was carried out in the Mokolodi Nature Reserve 24°45'S, 25°55'E, 15 km south of Gaborone in south-eastern Botswana. The reserve is about 4500 ha and fenced to keep wild animals in and livestock out. It was traditionally grazed by local livestock, and later served as a cattle ranch with heavy grazing until 1986 (Rooke 2003). It is located in a fairly hilly area and in the so called hardveld, covering a region in eastern Botswana consisting of rocky hill ranges and areas with shallow soil cover, where the dominating vegetation type is a mixed shrub and tree savanna. The vegetation types vary with the topography: *Combretum* shrub lands on hilltops and upper slopes, *Acacia* shrub lands on lower slopes, and *Spirostachys* woodland in bottom land along drainage lines (Skarpe *et al.* 2000). The reserve hosts 12 species of large herbivores (Tab. 1, nomenclature follows Alden *et al.* 1995), including four domesticated elephants. There are six species of browsing ungulates, (two browsers and four mixed feeders) and six grazers (Mokolodi nature reserve species list 2009) all earlier occurring in the wild in the region (Bråten 1997). The average annual rainfall in Gaborone (15 km from the reserve) is 538 mm mainly falling during summer, November-April. The field study was done in the end of the wet season, February-April 2008.

Table 1. Large herbivores at Mokolodi nature reserve, divided in browsers, mixed feeders and grazers. Population sizes and densities.

| Feeding technique | Species | | Population size | Density (individuals / ha) |
|-------------------|-----------------------------|---------------------------------|--------------------|----------------------------|
| | Common name | Scientific name | | |
| Browsers | Kudu, greater | <i>Tragelaphus strepsiceros</i> | 152 | 0.0338 |
| | Giraffe | <i>Giraffa camelopardalis</i> | 22 | 0.0049 |
| Mixed feeders | Eland, common | <i>Tragelaphus oryx</i> | 40 | 0.0089 |
| | Impala | <i>Aepyceros melampus</i> | 311 | 0.0691 |
| | Gemsbok / Oryx | <i>Oryx gazella</i> | 32 | 0.0071 |
| | Elephant, African | <i>Loxodonta africana</i> | 4, domestic | |
| Grazers | Wildebeest, blue | <i>Connochaetes taurinus</i> | 106 | 0.0236 |
| | Hartebeest | <i>Alcelaphus buselaphus</i> | 22 | 0.0049 |
| | Zebra, Burchell's | <i>Equus burchellii</i> | 74 | 0.0164 |
| | Rhinoceros, white | <i>Ceratotherium simum</i> | 9 | 0.0020 |
| | Hippopotamus, common | <i>Hippopotamus amphibius</i> | 2 | 0.0004 |
| | Waterbuck | <i>Kobus ellipsiprymnus</i> | 4 | 0.0009 |

Experimental set-up

The study was based on an enclosure experiment with three large, 11 year-old enclosures with corresponding unfenced controls. At the end of the wet growing season in 1997, three pairs of plots (each plot 150x150m) were subjectively located in the reserve, all three in the *Acacia* vegetation type. One in each pair was randomly selected for fencing (enclosure) and the other was left unfenced (control), i.e. open for grazing and browsing. The three sites were named 1, 2 and 3. The six plots were numbered 1 to 6, the controls having the even numbers and the enclosures having the odd numbers. Within each plot there was a buffer zone of 5 m along the fence/borders, resulting in a study area of 140 x 140 m. Each plot was then divided into 196 subplots (each 10x10m) and metal pegs were driven into the ground in each corner of the subplot. The sub-plots were named like the squares of a chess board, from "a1" to "n14" (Fig. 1). Before fence erection, a vegetation base-line study was conducted. All these data from 1997 form a data-base of some 37 000 trees (=trees and shrubs taller than 0.2 m).

Field work

The present study was conducted from February to April 2008 in the three sites established in 1997, described above. I compared enclosure and control areas in 1997 and 2008 with focus on density of trees (total density and differences within areas with low and high initial density), species composition and changes in proportion of a functional trait, spinescence. I also compared differences in spinescence within three species after 11 years of protection from large herbivores. Subplots were chosen randomly, with stratified random sampling. From a list with number of trees in each subplot from the study in 1997, I randomly chose subplots from the ones with densities close to 25% (considered low initial density, marked grey in Table 2) and 75% (considered high initial density, marked white in Table 2) of the highest densities in each plot. Eleven subplots with fewer or more trees were also selected during the first days of the field work, these were considered to belong to the density group they were closest.

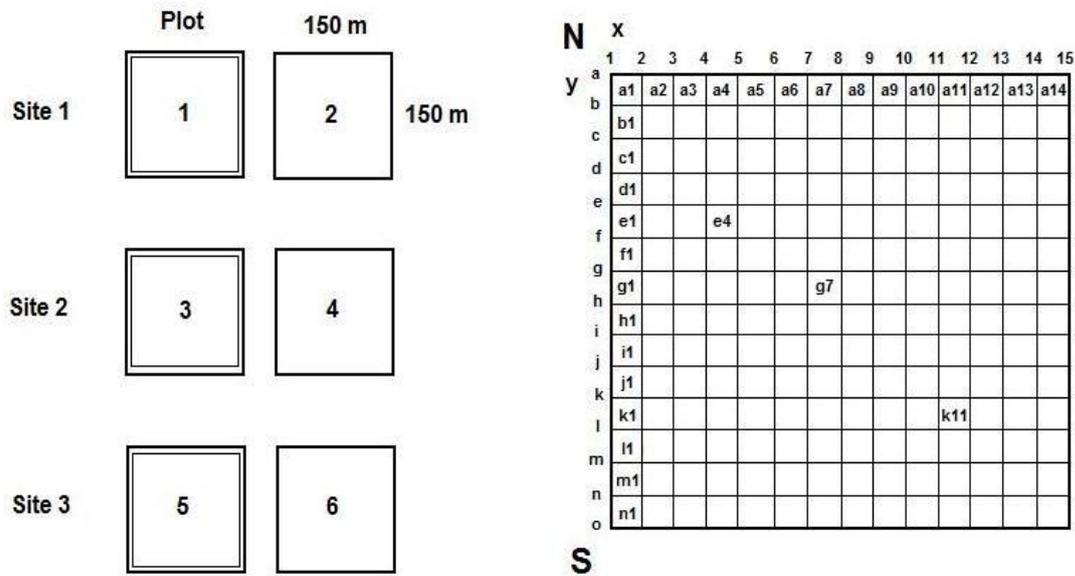


Figure 1. The study sites. 3 sites with 2 plots each, a fenced enclosure an unfenced control, and how all 6 plots (150x150m) are divided in 196 subplots (10x10m).

When a corner metal peg was not found for a subplot chosen, or found loose near to its expected place, surrounding pegs were used to estimate the lost peg's position. With help of a compass and tape measures 10 m was measured from the nearest north-south/west-east peg, also measuring the diagonal from the opposite corner peg to 14.1 m. The position of the lost peg was assumed to be where these three points met. If two or more pegs were lost another subplot was chosen. In total 114 subplots were examined, equally divided between the 6 plots (Tab. 2).

Tree density and species composition

Only woody plants higher than 0.2 m were recorded, and are referred to as trees. In cases where stems of the same species were growing close to each other they were considered separate individuals if the distance between their stems at ground level was longer than 0.2 m. In the base-line study conducted in 1997 the distance used to separate individuals was 0.5 m. For each tree, species was recorded according to the nomenclature in Coates-Palgrave (2002). Dead trees were considered of unknown species even if signs of spines etc. could be noted. Other variables were also recorded, but they have not been used in this report.

There were some uncertainties in species determination within the genera *Euclea* and *Maytenus*, which subsequently were lumped and treated as genus complexes. Even some of the small *Acacia* trees were difficult to determine to species as they neither had fully developed spines nor fruits. These acacias were simply called *Acacia* sp.

Functional trait: spinescence

The differences in proportion between spinescent and non spinescent trees were measured dividing all trees into two groups, “spines” (with spines, hooks or thorns, fig. 2 a-c) or “no spines” (without spines, hooks and thorns) and comparing the differences in proportion of spinescent trees between 1997 and 2008 in the control and the exclosure plots.

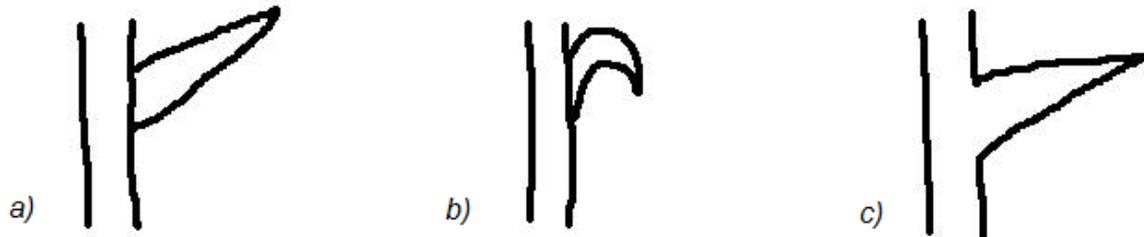


Figure 2. Illustration of a) spines, b) hooks and c) thorns.

Intraspecific differences: spines, hooks and thorns

The intraspecific differences in density of spines, hooks and thorns (Fig. 2 a-c) were measured counting and measuring these on three spinescent species in exclosure and control plots. The species included in the study were; *Acacia tortilis* (Ato, with spines and hooks), *Acacia caffra* (Aca, with hooks) and *Dicrostachys cineria* (Dci, with thorns); nomenclature follows Coates-Palgrave (2002). For each species 10 individuals were supposed to be selected and measured in each plot. In the first site we found 10 individuals for all 3 species in the control as well as in the exclosure plot. For the second site only three Aca were found in the control plot and five individuals were found in the exclosure plot. In the third site we found only one *A. caffra* in the control plot as well as in the exclosure plot. When an individual was found, 4 twigs were selected at random in north, south, west and east position of the canopy. All spines, hooks and thorns were counted on the first 10 cm of the twigs, seen from the twig apex. Four spines, hooks or thorns were also chosen randomly and measured on each twig chosen. When a twig chosen had less than four spines, hooks or thorns all spines, hooks or thorns present were measured. Some individuals within the species *A. tortilis* were completely devoid of spines or hooks on the twig chosen.

Statistical analyses

The plot was the sampling unit, and calculations are based on plot averages, given as numbers of trees per ha. Differences in density of trees, species composition and proportion of spinescent trees between exclosure and control areas, as well as intraspecific differences in density and size of spines, hooks and thorns in *A. caffra*, *A. tortilis* and *D. cineria* were analysed with Wilcoxon 1-sample nonparametric test in Minitab. Differences with $p < 0.05$ for the null-hypothesis were regarded as significant. The Wilcoxon 1-sample nonparametric test is a powerful alternative of 1-sample t-test that does not require any assumption for the distribution of the variable (e.g. when the assumption for normality is not satisfied).

Results

Tree density

I examined a total of 114 subplots (out of 1176 subplots included in the base-line study in 1997). I examined 18 subplots in plot 1, 2 and 5, 19 subplots in plot 6, 20 subplots in plot 4 and 21 subplots in plot 3. In total I examined 57 control subplots and 57 exclosure subplots. All subplots examined, except one, had a larger number of trees in 2008 than in 1997 (Tab. 2). The total number of living trees in the examined subplots in 2008 was 5664 compared

with 3234 in 1997. The total number of living trees examined and the tree density (trees/ha) in each of the 6 plots are shown in Table 3.

Table 3 Tree density and total numbers of living trees examined in all 6 plots (ex=exclosure, co=control), 1997 and 2008.

| Site | 1997 | | | | 2008 | | | |
|------|--------------------------------|------------------|--------------------------------|------------------|--------------------------------|------------------|--------------------------------|------------------|
| | ex | co | ex | co | ex | co | ex | co |
| | Total number of trees examined | Density Trees/ha | Total number of trees examined | Density Trees/ha | Total number of trees examined | Density Trees/ha | Total number of trees examined | Density Trees/ha |
| 1 | 622 | 3456 | 598 | 3322 | 1125 | 6250 | 1001 | 5561 |
| 2 | 688 | 3276 | 681 | 3405 | 1140 | 5429 | 1138 | 5690 |
| 3 | 298 | 1656 | 347 | 1826 | 589 | 3272 | 671 | 3532 |

The density of trees increased from 1997 to 2008 in all plots ($p=0.036$), but there were no differences in density between exclosure and control plots in 2008 ($p=1$) or in 1997 ($p=0.789$) (Fig. 3).

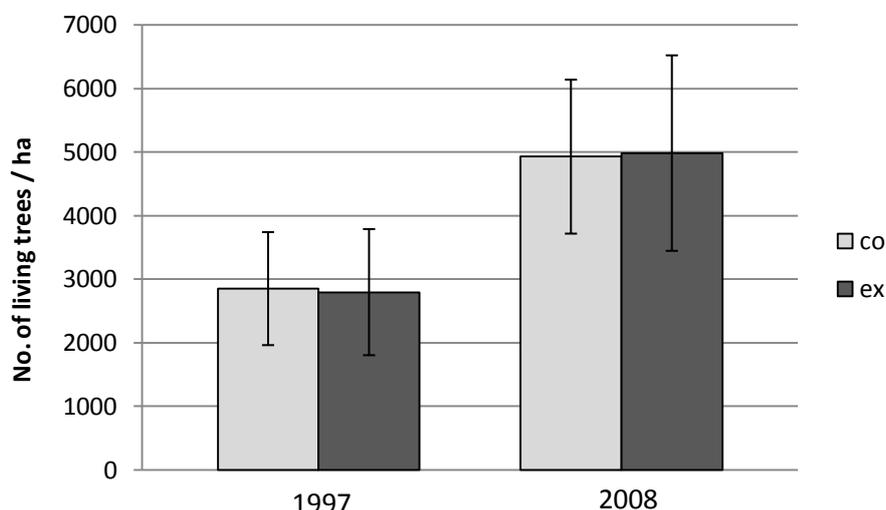


Figure 3. Density and standard deviation of living trees in exclosure (ex) and control (co) plots in 1997 and 2008.

Tree density in subplots with initial densities close to 25 and 75%

I selected subplots with densities close to 25% and 75% of the highest densities in each plot in 1997. Eleven subplots with fewer or more trees were also selected during the first days of the field work, but were considered to belong to either of the two groups. Fig. 4 shows the differences in density between 2008 and in 1997 in subplots with densities close to 25 and 75% of the highest densities in each plot 1997. No differences could be shown between exclosure and control plots neither in subplots with low initial density ($p=0.181$) nor with high initial density ($p=0.423$). Comparing exclosure subplots with initial densities close to 25% and 75% of the highest densities in each plot gave no significant result ($p=0.423$) and neither did comparing control subplots between subplots with densities close to 25% and 75% of the highest densities in each plot ($p=0.181$).

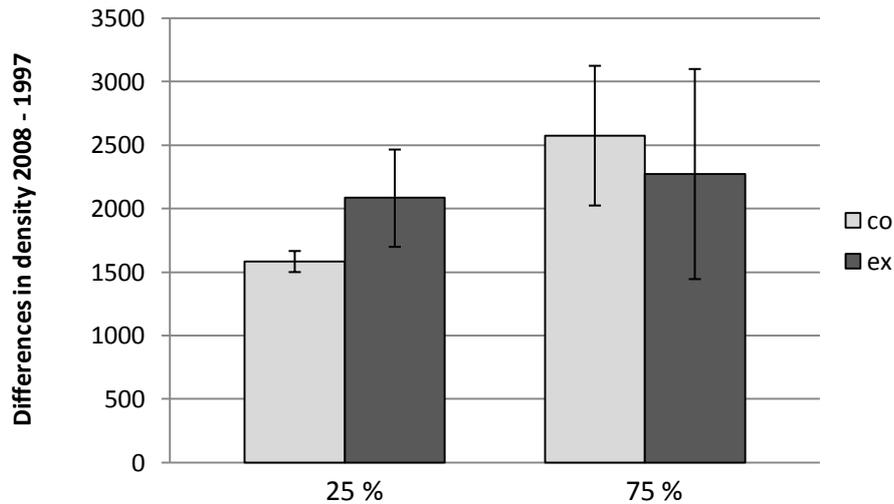


Figure 4. Differences between 2008 and 1997 in subplots with close to 25 and 75% of the highest densities in each plot in 1997.

Species composition

The survey comprised 35 species (*Euclea* spp. and *Maytenus* spp. were noted as one taxon each). The five most common species in 2008, both in the control and exclusion plots, were *Combretum apiculatum* (Cap), *Grewia bicolor* (Gbi), *Dicrostachys cinerea* (Dci), *Euclea* sp (Euc). and *Grewia flavescens* (Gfv). Together with *Rhus leptodictya* (Rle) and *Spirostachys africana* (Saf) they were the only species with more than 100 individuals totally, in 1997 or 2008, in the subplots examined.

Of these 7 species, *G. bicolor*, *C. apiculatum*, *G. flavescens* and *R. leptodictya* have a similar density increase in control and exclusion plots over the 11 years (Gbi $p=0.789$, Cap $p=0.423$, Gfv $p=1$ and Rle $p=1$). *D. cineria* seems to have a higher increase in density of trees in the control plots while *Euclea* sp. and *S. africana* seem to have a higher density increase in the exclusion plots, but the differences are not significant (Dci $p=0.181$, Euc $p=0.181$ and Saf $p=0.423$) (Fig. 5).

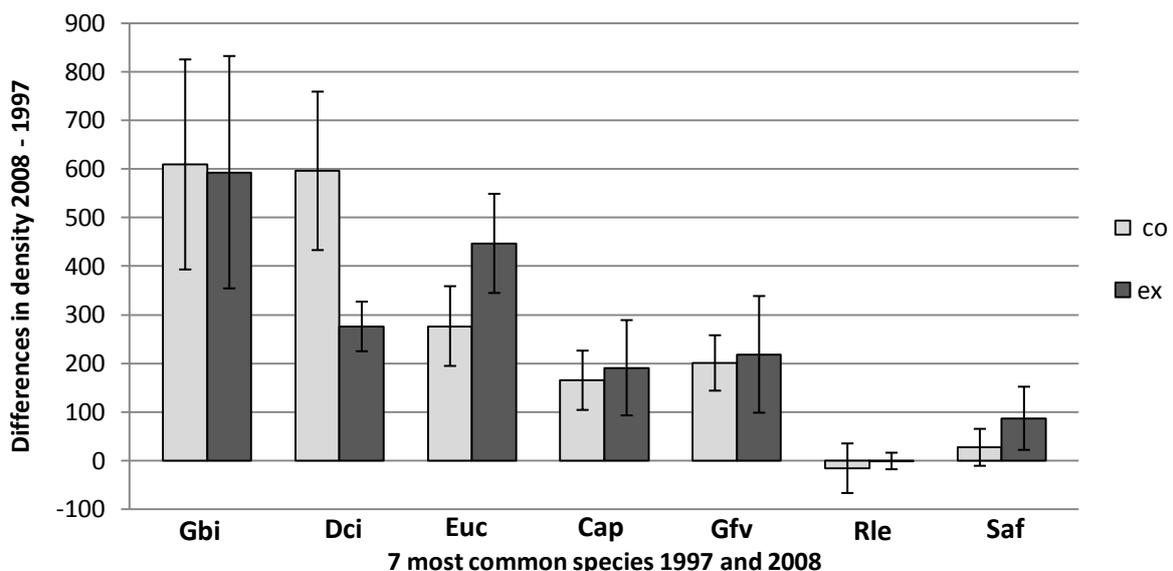


Figure 5. Differences in density (number of individuals per ha) and standard deviation 2008–1997 within the 7 most common species, *Grewia bicolor* (Gbi), *Dicrostachys cineria* (Dci), *Euclea* sp. (Euc), *Combretum apiculatum* (Cap), *Grewia flavescens* (Gfv), *Rhus leptodictya* (Rle) and *Spirostachys africana* (Saf), for both exclusion (ex) and control (co) plots.

Functional trait: spinescence, proportion of spinescent trees

I found no differences in proportion of spinescent trees between enclosure and control in 2008 ($p=0.423$) or in 1997 ($p=0.789$) (Fig. 6).

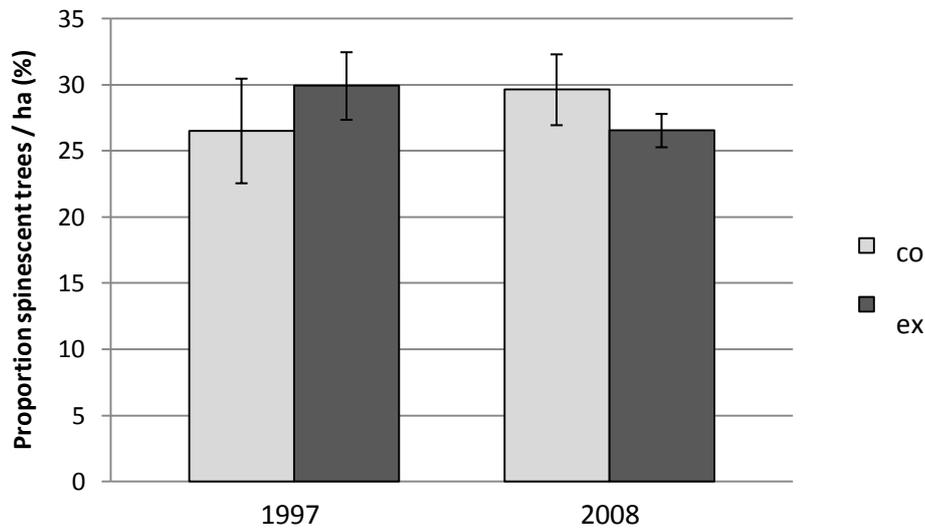


Figure 6. Proportion of trees with spines, hooks and thorns and standard deviation per ha (%) 1997 and 2008 in enclosure (ex) and control (co) plots.

Intraspecific differences: spines, hooks and thorns

There were no significant differences between enclosure and control plots in numbers of hooks per 10 cm twig in *A. caffra* ($p=0.423$), numbers of thorns in *D.cinerea* ($p=0.789$) or numbers of hooks and spines in *A.tortilis* ($p=0.423$ and $p=0.181$, resp.) (fig.7).

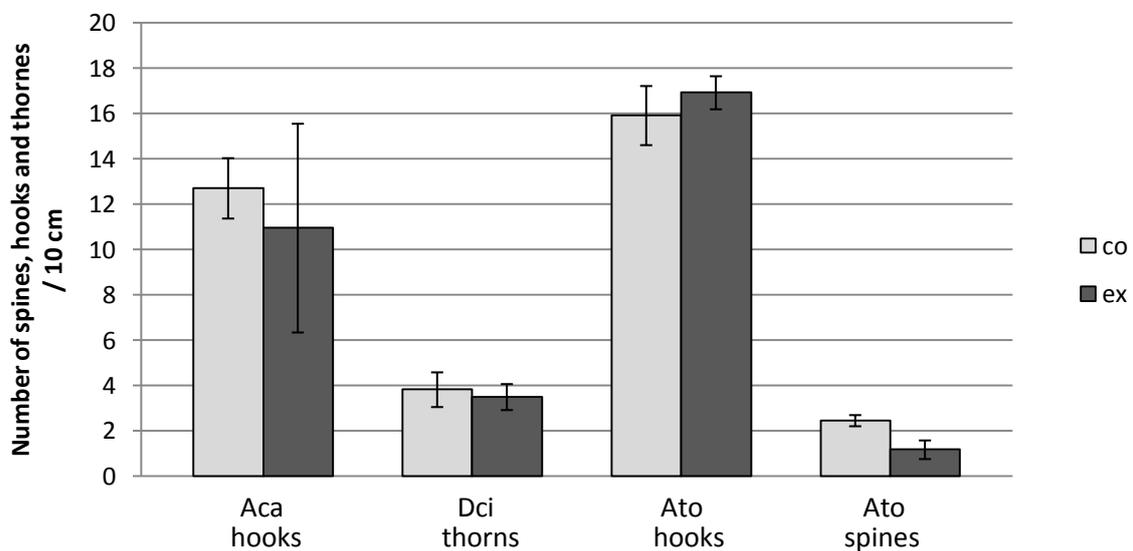


Figure 7. Mean numbers and standard deviation of spines, hooks and thorns on the first 10 cm measured from the twig apex on *Acacia caffra* (Aca), *Dicrostachys cinerea* (Dci) and *Acacia tortilis* (Ato) in enclosure (ex) and control (co) plots.

I did not find any significant differences between enclosure and control plots in mean spine, hook and thorn length (all species $p=0.423$) (Fig. 8).

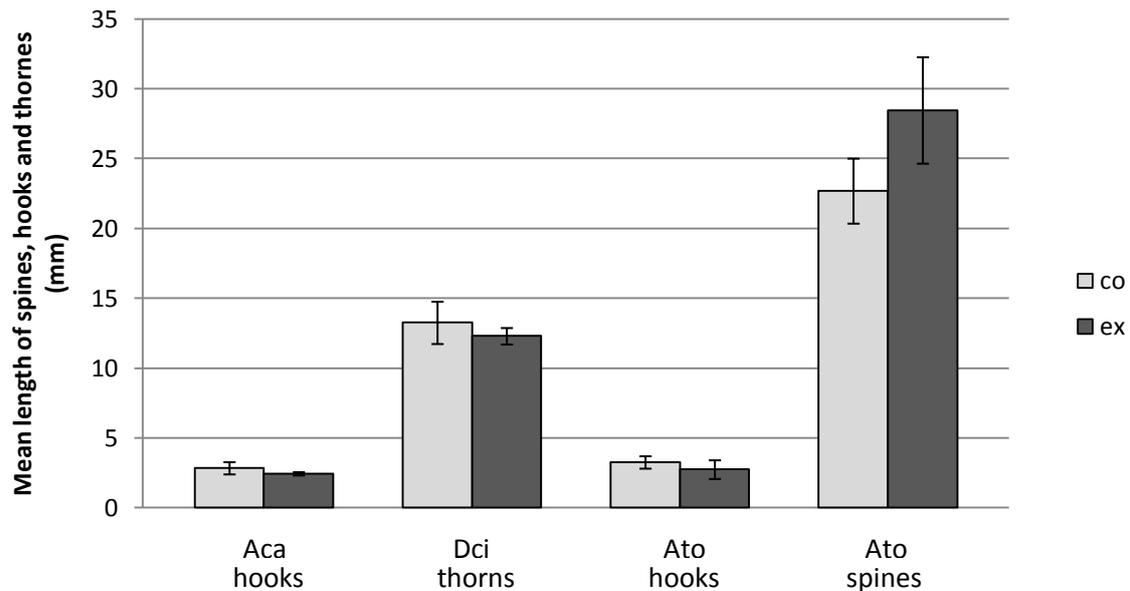


Figure 8. Mean length and standard deviation of spines, hooks and thorns on the first 10 cm measured from the twig apex on *Acacia caffra* (Aca), *Dicrostachys cineria* (Dci) and *Acacia tortilis* (Ato) in exclusion (ex) and control (co) plots.

Discussion

Tree density

The study revealed an overall increase in tree density since 1997. However, the increase of trees was not higher in the exclusion plots than in the control plots, as I predicted in my first hypothesis. The increase in trees in the control plots could be a result of bush encroachment. Bush or shrub encroachment is a worldwide phenomenon in savanna regions and the reason is often believed to be increased grazing levels and reduced use of burning to create grassland in combination with years of drought (Scholes and Walker 1993). Skarpe (1990) shows that in semi-arid areas with no or moderate grazing (and annual rainfall ca 350 mm), shrub densities fluctuate but do not show any consistent change, while shrub density increases with heavy grazing. Since I found a similar increase of shrubs and trees in both control and exclusion plots I can conclude that heavy grazing is not the reason for the increase in tree density in this case, at least not in the exclusion plots. However, until 22 years ago, Mokolodi served as a ranch with heavy grazing by livestock. Because of the repressive effect that the grass layer may have on young trees and old trees on grass layers, open savanna areas can convert to tree-dominated areas over a few years if the grass layer is weakened, for example by heavy grazing, it may take much longer time for the system to revert to the original state, and maybe it never does (Scholes and Archer 1997). So even after the removal of the cattle, trees and bushes can continue to dominate over grasses, which leads to a more wooded savanna (van Langevelde *et al.* 2003). One could therefore think that the vegetation at Mokolodi is in a phase resulting from the heavy grazing that the area was exposed to until 1986. The overall increase that I found in tree density could be a response to this heavy grazing by livestock in the past.

To date it is clear, that there is a general increase in woody growth that cannot be explained by heavy grazing alone. Ward (2006) and Britz and Ward (2007) mean that the processes and factors behind bush encroachment are a mixture between high temporal and spatial variation in rainfall, available soil nutrients and grazing pressure. Their theory implies that grass and tree biomass both increase with increasing rainfall under no grazing pressure. While under

heavy grazing the grass biomass per unit rainfall is reduced, reducing the competition with trees, which releases water and nutrient resources for trees to germinate. Since there is a greater possibility that trees will germinate when rainfall is higher, the differences between tree and grass biomass increases with increased rainfall. According to Ward (2006) this is proved by failed attempts to reduce bush encroachment by reducing livestock herds in dry years, indicating also that the problem to date is poorly understood.

The effects of fire on the savanna ecology are in many ways similar to those of herbivory (Bond and Keelay, 2005, Frost *et al.* 1986), in particular those of heavy browsing (van Langevelde *et al.* 2003). Fires affect grasses and trees differently. Grasses are favoured by fires since their apical meristem (growth zone) is located at the soil surface, just below the growing part (Skarpe and Hester 2008). Fires therefore do not damage the important part of the plant, but merely consumes the leaves. When grasses dry, much of their nutrients are relocated to the roots and they can easily re-grow lost leaves after a fire has burn the dried plant. Trees have their apical meristems at the tip of the shoots (Skarpe and Hester 2008) where they are vulnerable to fire, and are therefore not favoured by fires like grasses. Fires reduce woody vegetation by killing trees or reducing trees to smaller sizes (van Langevelde *et al.* 2003). Through these differential effects on grasses and trees a savanna protected from fires results in a savanna with increase in tree density and decrease in grass production (Frost *et al.* 1986). Within the Mokolodi nature reserve grass fires are not allowed to spread which could be another reason for the overall increase in tree density. Probably, within the area of Mokolodi nature reserve grass fires have not taken place for many years, because heavy grazing (like that of the livestock during the cattle ranch period) lead to fewer grass fires (Cheney and Sullivan, 2008). Since cattle prefer grasses over trees and bushes, the grass is held short and green which makes grass fires less frequent and intense, so the fires cannot reduce small shrubs and trees either. Through this mechanism, heavy cattle grazing leads to a savanna with increase in woody biomass (van Langevelde *et al.* 2003). According to van Langevelde *et al.* (2003) only woodland can occur with a low fire frequency and this equilibrium is stable until an increase in fire frequency occurs and leads to alternate stable states like savanna.

How interactions between herbivory and fire act to shape the savanna vegetation has been studied by Staver *et al.* (2009) in Hluhluwe iMfolozi Park, South Africa. They focused on impacts on sapling growth and seedling recruitment and found that fire and herbivory separate had no effect on seedling establishment and only small effects on sapling growth, but combined they had a much greater effect on sapling growth and therefore on tree density. They concluded that only fire and browsing together were able to prevent increase in tree density, which could be the reason that I found increase in tree density in both control and exclosure areas.

Abiotic factors (like water availability and soil texture) are also believed to play an important role for the vegetation in semi-arid savannas. Using data from 854 sites across Africa, Sankaran *et al.* (2005) showed that the maximum woody cover is constrained by the mean annual precipitation for savannas receiving less than 650 mm of rainfall per year. Also Shorrocks (2007) proposes that semi-arid and arid savannas are “climatically determined savannas” meaning that savannas with a mean annual precipitation of less than 650 mm depend on the precipitation for the coexistence between grass and trees, and not fire and herbivory even if they occur. In areas being fenced for 72 years (1906-1978) in the Sonoran Desert, Arizona, the total plant density and cover was significantly higher and most of the fenced plots had more than twice as many plants in 1968 as in 1906 (Goldberg and Turner

1986). It was concluded that the change in absolute cover and density most probably was a response to sequences of either extremely wet or extremely dry years. The study was an “exclosure exclusive study”, where fenced areas were not compared with unfenced control areas, but the results indicate that increase in density of plants can have other reasons than heavy grazing. Ward (2006) means that the slow growth rate of plants in arid and semi-arid regions and the high inter-annual variation in precipitation may cause negative, positive or non-existent effects of large herbivores on the vegetation. Thus short-term studies may be unable to reveal any effects of large herbivores on the vegetation.

Another important abiotic factor that affects the vegetation is the soil. In Kruger National Park, South Africa, the cover in woody vegetation has increased since 1940 in areas dominated by granite substrates (nutrient poor) and decreased on areas dominated by basalt substrates (nutrient rich) (Eckhardt *et al.* 2000). The increase in woody vegetation on granite substrates is believed to be a result of reduced competition with grasses after grazing by wild herbivores, while on the basalt substrates the grasses easily re-grow after grazing, probably due to the higher nutrient levels (Eckhardt *et al.* 2000). I have not taken in consideration any abiotic factors in this study and can therefore not tell how these have affected my results.

It should also be taken into consideration that in the base-line study conducted in 1997 the distance between individual trees was set to 0.5 m while in my study I calculated all trees with more than 0.2 m distance as separate individuals. This could have increased the density of trees in my results without actual increases in numbers of trees. However, species and genera likely to grow in clusters, like for example *Euclea* in general have less distance than 0.5 m between the boles (pers. observation) so I do not think that I have counted many more “separate individuals” than in the base-line study. Nevertheless my results do not show any differences in density of trees between exclosure and control areas. Maybe 11 years of exclusion of large herbivores is too short time to result in numeric changes in the vegetation or such changes in this savanna do not exist.

An example of a longer-term impact of herbivory along a rainfall gradient from annually 100 to 450 mm, is found in a study on effects of grazing on semi-arid ecosystems, by Ward and Ngairorue (2000) in Namibia. No correlation between the grass production and stocking density was found when looking over 11 years, but when data on grass production was compared for the same area over 58 years (1939–1997), grass production was shown to have decreased by approximately 50 %. This study clearly shows how different results may be obtained in long-term studies compared with shorter ones. It is possible that if this study is repeated in 40 years the results will be different.

Ward (2006) points out that change in vegetation density may be confounded with the effects of natural climatic variations (or even effects of human-induced global climatic change) on vegetation density. Human-induced global climatic change should therefore be considered when looking on changes in vegetation density. One example of human-induced global climatic change is the elevated levels of CO₂ in the atmosphere that also may have a positive effect on woody vegetation growth in grass-dominated ecosystems like savannas (Bond and Midgley 2000). In my study, I have not taken into consideration any climatic or atmospheric changes and can therefore not tell whether these could have influenced the results in this study.

I found the results surprising since visually there appeared to be much more trees and bushes in the exclosure plots than in the control plots. The reason could be that the trees inside the

enclosure plots were higher or had larger canopy, making it look like the tree density was higher, because young trees grow more rapidly in areas protected from both fire and herbivory, than in areas protected from fire alone (Frost *et al.* 1986). Andrea Herrera has looked into this issue in her master thesis (in prep.) and found that this is the case in Mokolodi nature reserve. The differences in mean height and mean canopy size between 1997 and 2008 for each subplot are smaller in the control plots than in the enclosure plots.

Tree density in subplots with initial densities close to 25 and 75%

I expected a higher increase in tree density in enclosure areas and also that there should be differences between areas with initial low and high tree densities, with higher increase in areas with initial low tree density. No such differences could be found between enclosure and control plots, neither in subplots with low initial density nor with high initial density, indicating that the exclusion of large herbivores neither has impact nor different impact on areas with low or high initial density. A tendency can be seen, although not significant (Fig. 4), that in subplots with initial low tree density the enclosure of large herbivores leads to a slightly higher increase in tree density compared with control areas. Comparing enclosure plots with each other did not show any differences, showing that in absence of large herbivores there is no difference in density increase between the areas with different initial density. But with large herbivores present (i.e. control areas) there is a slight difference (not statistically significant) in Fig. 4 between control plots with densities close to 25% and 75% of the highest densities in each plot. This result could indicate that under conditions with large herbivores present the tree density in this semi-arid savanna possibly increases more in areas with already high initial density. This is contrary to what I presumed in my hypothesis and to what the models by Guo *et al.* (1998) predict. The fact that there is a higher increase in tree density in areas with initial high tree density shows that self-thinning due to tree-tree competition probably not takes place in these areas. The reason for this could be that tree density is not high enough to cause competition for the resources. If it was, there should not be an increase in tree density within areas with initial high tree density, but a possible decrease. Or a high initial density of trees, in this case, simply creates a higher increase in tree density because more seeds are produced and therefore a bigger amount is falling down on the ground, where they are in an environment protected from large herbivores (i.e. under bigger plants) facilitating germination.

Species composition

C. apiculatum, *G. bicolor*, *G. flavescens*, *R. leptodictya* and *S. africana* showed similar increase in density, independent of treatment. In a browsing study conducted in 2000 in Mokolodi Nature Reserve, Sjögren (2000) showed that *C. apiculatum* is preferred by browsers, whereas *G. bicolor* was rarely utilized during the wet season but appeared to be browsed during the dry season. *G. flavescens* is a species low in chemical deterrents and is highly acceptable to mammalian browsers (Scholes and Walker 1993). *Rhus* spp. was in a study at Mokolodi conducted by Skarpe *et al.* (2000) among the five taxa with the highest relative utilization. Despite its poisonous latex (Coates-Palgrave 2002) also *S. africana* is a popular food source for many large browsers on the savanna (Skarpe *et al.* 2000). According to my second prediction these five species preferred by large herbivores should have increased more in the plots, where they are not exposed to browsers. Possibly the relatively low herbivore density within the nature reserve leads to a low browsing pressure that maybe could be compared to that in areas with herbivore oscillations (basically changes in browsing/grazing pressure over time). The oscillations allow previously used resources to recover, avoiding negative density-dependent effects of herbivory on plant biodiversity (Ward

2006). In this case the low browsing pressure, allowing the vegetation to recover, could result in the same plant biodiversity in control and exclosure plots.

In line with my third prediction, *D. cineria*, a species protected by thorns but still favoured by browsers (Scholes and Walker 1993, Sjögren 2000), may have increased slightly more in the control plots where it is exposed to browsing compared with the exclosure plots (even if the difference is not statistically significant). *D. cineria* defends itself against herbivory with thorns and may benefit from the reduced interspecific competition that is the result of the browsing pressure. It is also a pioneer or invasive species that tend to colonise early successional sites (Obiri *et al.* 2002) and therefore probably benefits from herbivory. *D. cineria* was found to be the only species recruiting seedlings regardless disturbance such as herbivory and fire in a model test in Hluhluwe iMfolozi Park, South Africa (Staver *et al.* 2009).

Species belonging to the *Euclea* genus are early-successional shrubs with the potential to facilitate natural forest regeneration by protecting seedlings against grazing and browsing. They have in the past been classified as invasive weeds, responsible for bush encroachment (Aerts *et al.* 2006). In Mokolodi Nature Reserve the *Euclea* genus is rarely utilized by browsers during the wet season but appears to be somewhat browsed during the dry season (Sjögren 2000). *Euclea* sp. showed a slightly higher increase (not significant) in density of trees in the exclosure plots than in the control plots, thus possibly having increased more when protected against browsers, even if they are not much selected for by browsers and not all year around. However, for a species that is not preferred by browsers I would not expect this to be the reason for the increase. It is more probable that such an increase does not exist here or was caused by other factors, not investigated in this study.

In the exclosure study in the Sonoran desert Goldberg and Turner (1986) did not find any strong differences in species composition over time. They could only find two species (*Krameria grayi* and *Janusia gracilis*), both very palatable to livestock, that appeared to increase continuously in the fenced areas under the study period. Scholes and Archer (1997) establish that species composition relationships are influenced by a variety of factors, including grazing, browsing and rainfall, so maybe herbivore exclusion alone is not affecting the species composition as I expected.

Functional trait: spinescence

Herbivory did not have any effect on sapling growth when Staver *et al.* (2009) looked on species separately in Hluhluwe iMfolozi Park, but when species were pooled into functional groups they found results to be significant. When I divided all my examined trees in two functional groups (spinescent and non-spinescent trees) I found a slight decrease in the proportion of spinescent trees in the exclosure plots since 1997 (Fig. 6) (no differences could be shown statistically). Such a result would correspond with what I predicted in my hypotheses. Supporting my weak results, in a study made by Noy-Meir *et al.* (1989) spinescent plants were not more frequent among plants increasing with increasing herbivory, and chemical palatability was found not to be a major factor determining plant selection by herbivores. In fact they found a trend, although not significant, in the opposite direction.

Intraspecific differences: spines, hooks and thorns

I found no evidence for the number of spines or the spine length being an induced defence in any of the spinescent species studied. Previous studies have shown increased biomass of spines on acacia trees subjected to browsing or clipping compared with non-browsed trees

(Rooke 2003, Shorrocks 2007, Young *et al.* 2003), but also results similar to mine (Rooke *et al.* 2004). My result for the numbers and length of spines, hooks and thorns is, however, not consistent with my hypothesis, showing that number and length were not related to herbivore exclusion. Maybe there is some ulterior factor affecting the spine length in these species that I have not looked into. In areas in Kenya the spine length on new shoots of *Acacia drepanolobium* decreased with 35-40% after excluding herbivores only on individuals occupied by the ant species *Crematogaster mimosae*, while other individuals occupied by another ant species, *Crematogaster nigriceps*, did not show any differences in spine length between browsed and non-browsed areas (Young *et al.* 2003). This result clearly shows that spine length in *A. drepanolobium*, and maybe in other acacia species can be influenced by large browsers, but also that aggregated factors may cause different results. In the same study the authors also found that the spine length responses to herbivores were extremely local, in fact limited to individual branches. Other spinescent species that have been found to form shoots with more spines after being exposed to browsing are bramble (*Rubus fruticosus*) and holly (*Ilex aquifolium*) (Bazely *et al.* 1991, Obeso 1997) indicating a possible ability to increase defence against browsing once being exposed to it. I believe I could have reached different results by collecting more specimens from each species and also by measuring more spines on each individual tree. The problem that I had in finding 10 individuals of each species in each plot could have been resolved in advance, if studying the base-line study from 1997 where these species grew more exactly; now I lost time walking around within the plots looking for specimens. It is also probable that the browsing pressure is too low within the nature reserve to have any effect on density of spines and spine length in these species, like described above.

Concluding remarks

The large herbivores within the nature reserve did not have the effect on the savanna ecosystem that I expected. The only significant difference that I could find within my study site since 1997 was the overall increase in tree density. It seems like this change does not have anything to do with the exclusion of large herbivores, but could depend on the fact that humans control the fire regime within the nature reserve. Another possible cause to the overall increase in tree density could be an increase in the atmospheric CO₂ since 1997 or further a local or global climatic change, resulting in for example either extremely wet or extremely dry years. In this study designed to examine changes caused by large herbivores, only changes possibly caused by humans were revealed. Probably we, humans, are the ones affecting the ecosystems that we are protecting, studying and learning from, more than the animals and organisms living there are!

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