



Examensarbete i ämnet biologi

Herbivory on woody plants and induced responses in two similar species of Acacia in the Kruger National Park, South Africa

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ABSTRACT

I studied browsing patterns and the effects of browsing by different groups of herbivores on woody plants in Kruger National Park in South Africa. I determined how the browsing pressure varied with distance to water and measured inducible responses on two species of Acacia (*A. exuvialis* and *A. grandicornuta*).

The experimental approach involved excluding herbivores by the use of fences. Three treatments were used; a full enclosure (FE, excluding all mammals larger than hares), a partial enclosure (PE, excluding elephants and giraffes) and a control area (NE, no exclusion). Two vegetation types were distinguished, related to the crest (further from the river) and the footslope (closer to the river) within the study site. Thirty transects were randomly placed in each treatment (15 on each vegetation type) and the woody plants in each transect were counted and measured. Spines, leaves and shoots were measured on one selected Acacia individual in each transect. In NE and PE browsing severity was estimated on all individuals < 150 cm.

Results show that browsing was greater on footslope than on crest, and greater where all herbivores had access to the plants compared to where elephants and giraffes were excluded. Effects of elephant exclusion were greater on crest than on footslope. Some evidence of inducibility of plant responses was found. Spines were 39 % shorter in FE compared to NE for *A. exuvialis*, but leaf lengths seemed to increase with exclusion of herbivores. A strong positive correlation was found between shoot length and spine abundance, but because of heavy rain near the end of fieldwork, shoot lengths and spine abundances were greatest in PE.

The effects of elephants on the woody plants of the savanna ecosystem demonstrated in this study are alarming when considering the rapidly growing populations of elephants and the potential damage they can cause. The greater effect of elephant exclusion I found on the crest is a result which would be interesting to incorporate into elephant management. Long spines and short leaves make plants less attractive to mammalian herbivores and this is very important to consider in the widespread and growing utilization of savanna vegetation as food for livestock, because if the sizes of elephant populations continue to increase, the competition between wildlife and livestock for the savanna ecosystem will do the same.

1. INTRODUCTION

The widespread occurrence, and in most cases nonlethal effects of herbivory on terrestrial plants, indicates that in many ecosystems the majority of plants are adapted to herbivory (Ohgushi 2005). There are numerous different ways in which herbivores can affect plants (Maschinski and Whitham 1989) and many diverse ways that plants can defend themselves (Hanley et al. 2007). But defences can be costly (Herms and Mattson 1992), so in cases when herbivory varies in time or space it might be favourable for the plant to use inducible defences (Young et al. 2003). That way the rate of herbivory can be matched by an equally strong defence and resources do not need to be invested in defence all the time. Many authors consider spines and thorns to be a part of such an inducible defence, and various studies have shown results in support for this. Thorns have been shown to reduce herbivory by decreasing bite sizes and biting rates (Cooper and Owen-Smith 1986), and removal of thorns has resulted in increased levels of herbivory (Wilson and Kerley 2003, Cash and Fulbright 2005). Branches located above browsing heights (Young 1987, Milewski et al. 1991, Young et al. 2003) and plants in areas protected from herbivory (Obeso 1997, Rhoner and Ward 1997, Young and Okello 1998) have displayed reduced thorn sizes in comparison with branches and plants exposed to herbivory.

The general idea is that longer or more abundant spines will be better capable of protecting leaves or other parts of the plant desired by herbivores. But as pointed out by Cooper and Owen-Smith (1986), the success in herbivore deterrence would also be dependent on the size of the leaf in question. Consequently, if one wants to study the induced responses of spines to herbivory, and how effective they are in reducing herbivore damage on leaves, leaf size measurements should be included. However, the timing of damage (e.g. early or late during growing season has a strong effect on leaf growth response (Hjältén et al 1993). In this study, the accumulated effects of many years of browsing on physical traits of plants are considered, which means that the specific browsing pattern during the most recent seasons is less important.

Despite the fact that spines and thorns can be easily manipulated and measured in the field (Young and Okello 1998), they have received little attention in comparison with other inducible defences such as chemical compounds (Grubb 1992) and growth form (Campbell 1986). In a review on plant resistance to herbivory made by Boege and Marquis (2005) only one out of 17 papers on direct defence included a structural element. In addition, the role of spinescence as a defence against herbivores is still questioned (Hanley et al. 2007), and it is not always clear how effective spines and thorns are against herbivory (Belovsky et al. 1991). If we are to fully understand the role of induced defences against herbivory more research is needed on the subject.

The overall occurrence of spines on plants is a common feature (Milewski et al. 1991), especially in Africa where species of the genus *Acacia* are abundant (Grubb 1992). This group of plants is a very important part of the woody plant community in savannas (Midgley and Bond 2001), and Goheen (2007) points out studies linking them to such important factors as productivity, species diversity, soil-water infiltration and availability of nutrient pools. They also play a role in the heavily debated phenomenon known as bush encroachment (Midgley and Bond 2001), which is an increase in the density of woody plants (often unpalatable by domestic livestock), typically resulting in impenetrable thickets which suppress palatable grasses and herbs (Smit 2004). Both the *Acacia* dominance and spinescence in African savannas are considered to be results of herbivory by large mammals (Augustine and McNaughton 2004). This makes them ideal when studying the

induced defences of herbivory on plants, as they might provide an insight into some of the important processes governing these defences.

Another response to herbivory is compensatory growth (Strauss and Agrawal 1999), such as regrowth of browsed shoots (Du Toit et al. 1990). The theory is that when a shoot or leaf is browsed, the remaining ones experience a reduced competition for nutrients (Moorby and Wareing 1963). They will then obtain a higher concentration of nutrients and together with the breaking of apical dominance this will cause them to grow (Du Toit et al. 1990, Hjältén et al. 1993). Several studies have even recorded overcompensation in some Acacias (Du Toit et al. 1990, Dangerfield and Modukanele 1996, Gadd et al. 2001). In this study, we investigate if shoots and leaves protected from browsing display less growth than those on plants in currently browsed areas.

When it comes to wildlife management, especially on the savanna, there are few other aspects more widely or strongly debated than those concerning elephants (Cadman 2005). There has been extensive research done on elephants, but very few studies have focused on their potential effects on spines and other inducible defences. In a review made on elephant research in 1998, Bossen concluded that 93 out of 1059 studies looked at elephants and vegetation, but the great majority of those studies were conducted in the eastern part of Africa, and only 4 in South Africa (one of the places where the elephant debate has been most intense). In addition, more needs to be known about how woody plants respond to the utilization by elephants (Styles and Skinner 2000).

One of the protected areas in South Africa where elephants can be found is the Kruger National Park (KNP). Since the decision made by SANParks (South African National Parks) in 1995 to stop all culling of elephants in the parks under their management, the elephant population in KNP has grown rapidly (Whyte 2005) and results from the 2006 census put the population at about 12400 individuals (Blanc et al. 2007). Concerns have been expressed as to whether expanding populations of elephants might cause losses in biodiversity (Baxter and Getz 2005) and results from many studies indicate that such concerns are justified (Moolman and Cowling 1994, Cumming et al. 1997, Fenton et al. 1998, Lombard et al. 2001, Botes et al. 2006).

Brits et al. (2002) studied impacts of large herbivores on woody vegetation close to two water holes in KNP. They found that the density of woody plants was much lower closer to the watering points, with a logistic increase away from one point, and a constant increase away from the other. Smit (2007) analyzed aerial census data sets on elephant distribution in KNP for 1987-1993, and found that elephants in the park aggregate around rivers during the dry season. The question raised here is if the patterns in browsing found close to water holes can also be seen near the rivers, and if so, what effects of this can be seen on browsing severity and on the inducible defences of the woody plants in the area.

In this study, exclosures were used to exclude herbivores, but they were based on animal height. As a result, the fences used against elephants also excluded giraffes. Giraffes do not have the same potential of affecting vegetation as elephants. In general, their ability to affect populations of trees is small compared to other megaherbivores (Owen-Smith 1988) but Milewski et al. (1991) state that "It is reasonable to suggest that thorniness in East African acacias functions today mainly as a defence against giraffes", so their possible effects are not to be neglected.

This study focused on browsing of woody plants in KNP, how it varies with distance to the Sabie river, and induced responses in two different species of Acacia. This was achieved by selectively excluding different herbivores with different types of fences and surveying the vegetation using transects. The aim of this study was to address the following questions: A) How does the absence/presence of giraffes and elephants affect overall browsing severity? B) Is the severity in browsing dependent on the distance to water? C) How does the presence/absence of elephants and giraffes, and other large herbivores affect the length of shoots and leaves, and the abundance and length of spines?

More specifically, the following was hypothesized:

- A. Exclusion of elephants and giraffes will lead to lower levels of browsing.
- B. The browsing pressure is greater close to water.
- C. Spine lengths (defence) will decrease with the exclusion of elephants and giraffes and more so with exclusion of all large and medium sized herbivores.
- D. Spine abundance (defence) will decrease with exclusion of elephants and giraffes, and more so with exclusion of all large and medium sized herbivores.
- E. Leaf lengths (growth response) will decrease with exclusion of elephants and giraffes, and more so with exclusion of all large and medium sized herbivores.
- F. Shoot lengths (growth response) will decrease with the exclusion of elephants and giraffes and more so with exclusion of all large and medium sized herbivores.

2. METHODS

2.1 STUDY SITE

Fieldwork was carried out between 15 Nov and 12 Dec 2007 in the Nkuhlu exclosures (Figure 1). The site is situated in the southeast part of Kruger National Park, on the northern bank of the Sabie river (25°0' N, 31°45' E). The area is characterized by bush savanna on granite bedrock with sandy soils. Annual rainfall varies around 550 mm per year with the majority falling during the raining season Oct-Apr. Elevation is roughly 200-230 m. The exclosures were erected in 2002 and designed to determine the effects of fire, elephants and other herbivores on the vegetation (O'Keefe and Alard 2002). They comprise an area of about 25-30 ha each, and consist of two different types of fences: the full exclosure (FE); which excludes all mammals larger than hares, and the partial exclosure (PE); which excludes only elephants and giraffes (any animals taller than 1,8m). Between the two exclosures there is a control area (NE) which can be accessed by all animals. The study area lies on a slope close to the river, from higher ground (crest) in the eastern part down towards lower ground (footslope) in the western part. The vegetation on the crest is dominated by *Dichrostachys cinerea* and *Combretum* species with some abundance of *Commiphora africana*, *Acacia exuvialis* and *Grewia flavescens*. The footslope vegetation has fewer abundant species and is heavily dominated by *Acacia grandicornuta* and *Rhigozum zambesiaccum*. In the study area there are a few fire breaks (tree free roads capable of restraining the spread of fire) used for studies on fire dynamics. The mammal fauna frequently visiting the Nkuhlu area is diverse (pers. obs.) and common herbivores include elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), impala

(*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis*), buffalo (*Syncerus caffer*) and hippopotamus (*Hippopotamus amphibius*).

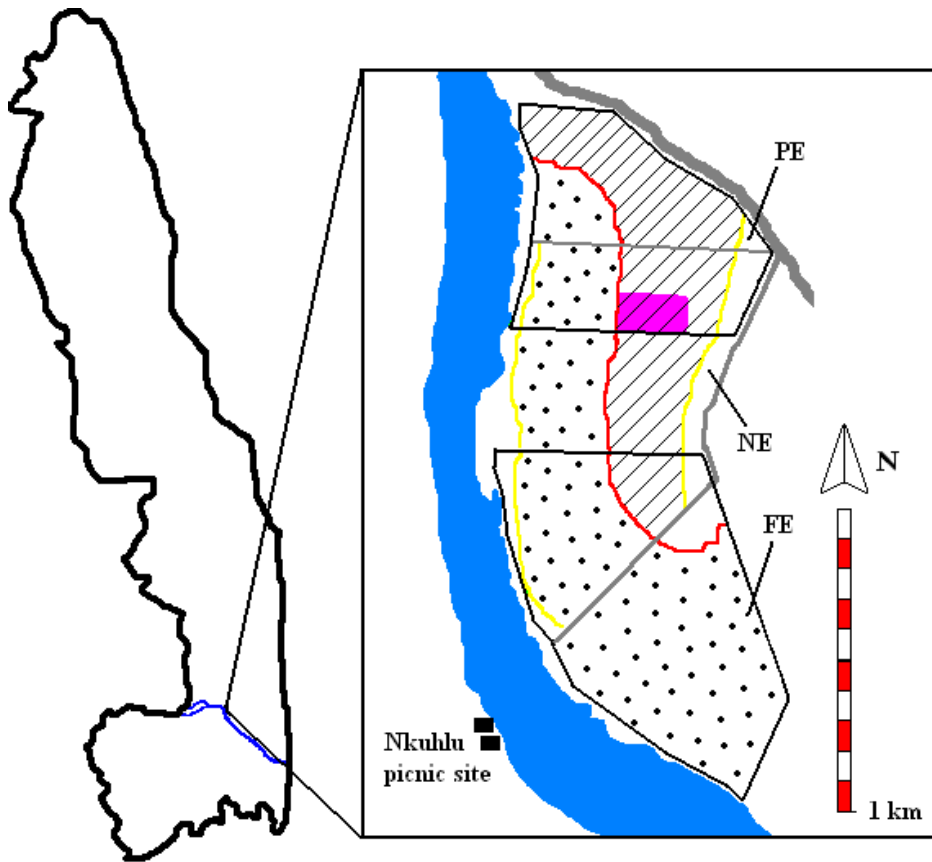


Figure 1: Study site

Map of the study area close to the Sabie river (Blue field) in the south of Kruger national park. Roads and fire breaks are indicated with grey color. The dotted area is the footslope vegetation and the striped area is the crest. The border between the two vegetation types is shown with a red line. Yellow lines indicate the eastern border of the crest vegetation and the western border of the footslope vegetation. Fences are marked out with black lines, with the partial enclosure far north, the full enclosure far south and the control between them. The pink area symbolizes a patch of vegetation greatly deviating from its surroundings which could not be used in this study.

2.2 ACACIA SPECIES

The two Acacia species studied were *A. exuvialis* (Flaky-bark Thorn) and *A. grandicornuta* (Horned Thorn). They are both fairly common species in the area, but *exuvialis* grows mainly on the crest of the study site and *grandicornuta* is found almost exclusively on the footslope. Both species have paired hollow spines developed from leaf-stipules and pinnately compound leaves. *A. exuvialis* has a maximum height of 5 m, and *A. grandicornuta* can reach 12 m (Schmidt et al. 2007), but in this area Acacias of this size are rare.

2.3 TRANSECT SAMPLING

Thirty 2x40m transects were randomly placed in each of the three treatments (15 on crest and 15 on footslope) using a fixed grid with squares of roughly 30 x 30 m, and the starting points for each transect at the centre of each square. All transects were placed north of the fire break in FE and south of the fire break in PE, and well within the borders of each vegetation type. A few parts of the study area had to be excluded from the study: Some were situated close to fire breaks or fences and could be affected by the bordering treatments, so no transects were placed within 30 m from these structures. One part of the crest in PE had vegetation similar to that on the footslope part of the same treatment (Figure 1). In order to avoid a biased result, that patch of vegetation was also excluded. Between crest and footslope vegetation in all treatments a 30 m border was set, where no transects were placed, so that there would be a clear distinction between the two vegetation types.

The transect starting points were located using a GPS. On site, a compass was used to pull the transect chain in a straight line towards the magnetic north. In all three treatments every woody species of shrub and tree with the stem within one meter from the chain and with the potential of growing into the tree layer (without support from other plants) were then used. On these individuals, recordings of species and height were made. Stems more than 50 cm apart were considered separate individuals. In PE and NE, browsing estimations were also made on individuals shorter than 150 cm. This height was chosen to include the herbivory of non-mega herbivores, which almost only feed below a height of 2 m (Young et al. 2003). Since no large herbivores had access to FE, recent browsing by mammals was absent and no browsing was estimated in that treatment. Browsing estimations made in NE and PE included leaf herbivory (% of total leaf area lost), number of unbrowsed/browsed shoots (except where there were too many shoots to count, in which case an estimation was made on percentage browsed shoots) and accumulated browsing (% total biomass above ground lost). Only browsing by mammals was recorded and shoots were only recorded as browsed when the apex had been removed. For the accumulated browsing no distinction was made between actual browsing and breakage, since elephants can break branches and stems to gain access to certain parts of a plant. There are problems with browsing estimations such as these. First there can be differences depending on who does the estimation, which was avoided by ensuring that the same people did the estimates in all treatments. Secondly a plant may have been browsed in the past but in such a way that it is very difficult to see, and as a result there might be a slight over estimation of unbrowsed individuals. But since the focus of this study is to compare effects between treatments and between vegetation types, and because possible over estimations should be similar in both treatments, the negative effects from this are probably small.

The first individual of *Acacia exuvialis* (on crest) or *Acacia grandicornuta* (on footslope) in each transect was chosen for shoot measurements. Individuals were not chosen if taller than 150 cm or if the accumulated browsing exceeded 50 %, because taller trees would be difficult to measure, and previously very heavily browsed trees could be too damaged to respond to treatment effects. The selected plants also had to have at least five measurable annual shoots. In cases where no such tree could be found within the transect, the suitable tree closest to the transect starting point (without entering the vicinity of another point) was selected. On the chosen individual, 5-10 annual shoots were selected randomly (the number depending on how many could be found). On these shoots, measurements of shoot length, longest leaf, no. of spines and the longest spine in each pair of spines were taken. On the shoots there were very short, undeveloped spines which were hard to distinguish and measure. Depending on who selected and measured these spines

there could be great differences in length and number of spines. In order to eliminate this problem all spines shorter than two mm were excluded, so that there would be a clear distinction between what should be recorded and what should not. Shoot length was measured from the shoot base to the base of the bud, and spine length from spine base to spine tip (Figure 2). The leaves of the two Acacias are pinnately compound and when exposed to higher temperatures they fold the pinnae towards the rachi to minimize water loss (pers. obs., Figure 2). This causes the total length of the leaf to fluctuate during the course of the day. To minimize the effects of this behaviour, the length of each leaf was measured from the base of the petiole to the base of the terminal pinnae.

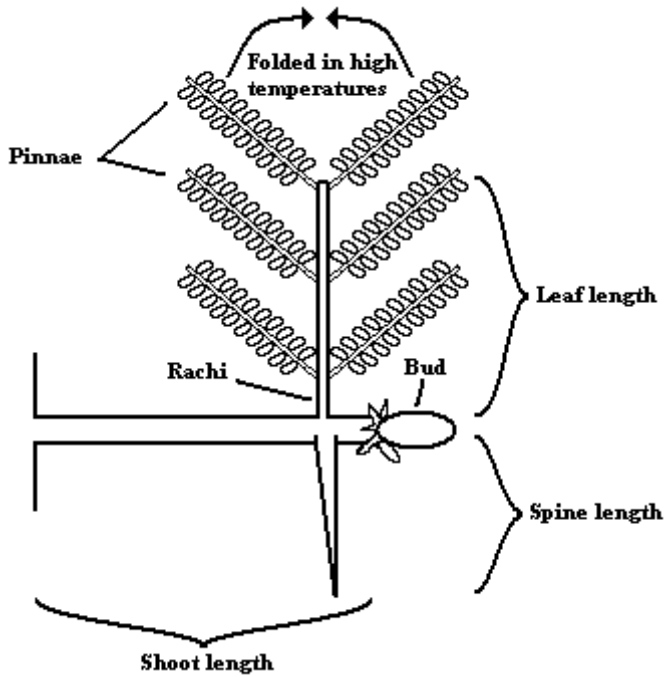


Figure 2: Measurements of induced responses

This sketch shows how measurements of shoot, spine and leaf lengths were taken on the two Acacias. If temperature is high the pinnae fold up against the rachi, and this causes the leaf length to vary during the day. To prevent biased results, the leaf length was measured from the petiole base, to the base of the terminal pinnae. Shoot length was measured from shoot base to the base of the bud, and spine length was measured from spine base to spine tip.

2.4 STATISTICAL ANALYSIS

Data analysis was done using JMP version 7.0.1 (SAS Institute 2007). In order to perform the required analyses, measurements of spine length, spine abundance, leaf length and shoot length were used to calculate a mean for each individual plant, which were used as replicates.

The square roots of leaf and shoot lengths were taken before analyses to closer fit requirements for normal distribution and equal variances, and then analyzed using One-way ANOVAs for overall effects and Tukey HSD for pairwise comparisons. Data on spine length, accumulated browsing and number of spines deviated from normal distribution and/or equal variances and could not be transformed satisfactory, and was therefore analyzed using a nonparametric Wilcoxon test for both overall effects and pairwise comparisons. The relationship between shoot length and spine abundance was analyzed using a linear regression analysis so as to assess how related these factors are.

In this study only mammal browsing was recorded, but because of the difficulty to distinguish between mammalian and insect herbivory on leaves and shoots, herbivory was only recorded when the type of herbivore responsible for the damage could be established with certainty. This, together with few shoots and leaves being browsed overall, resulted in very few recordings of browsing on shoots and leaves, and as a result, it was not possible to perform satisfactory analyses on leaf stripping and annual shoot biting. To obtain a better overview of the accumulated browsing, the number of unbrowsed (0 %) individuals was compared between treatments.

3. RESULTS

3.1 WOODY PLANT ABUNDANCE

The abundance of woody individuals found in each treatment and vegetation type can be seen in table 1. There was great variation between vegetation types, greater numbers of woody plants were found on crest than on footslope. When comparing treatments, FE had more individuals than the other treatments on the footslope vegetation, but fewest individuals on crest.

**Table 1: Abundances of woody plants
(individuals / m²)**

Treatment	PE	NE	FE
Veg. Type			
Crest	4,42	4,10	3,70
Footslope	2,45	1,94	2,80

3.2 BROWSING

The proportions of individuals shorter than 150 cm (on which browsing was estimated) were comparatively consistent between both treatments and vegetation types. In PE they made up 66 % and 64 % on crest and footslope respectively. In NE the percentage was slightly higher with 70 % on crest and 75 % on footslope.

The mean accumulated browsing was greater in NE than in PE, for both crest (Wilcoxon $p = 0,0191$) and fotslope (Wilcoxon $p = 0,0214$) vegetation (Figure 3). Browsing on fotslope vegetation was more severe than that on crest, in both PE (Wilcoxon $p < 0,0001$) and NE (Wilcoxon $p < 0.0001$). So the hierarchy from most browsed to least browsed is as follows; NE fotslope (19,6%), PE fotslope (17,5%), NE crest (16,0%) and PE crest (8,9%). This means that the difference in browsing severity between NE and PE (i.e. the effect of elephant exclusion) is more than three times as great on crest compared to fotslope (7,1 % vs. 2,1 %).

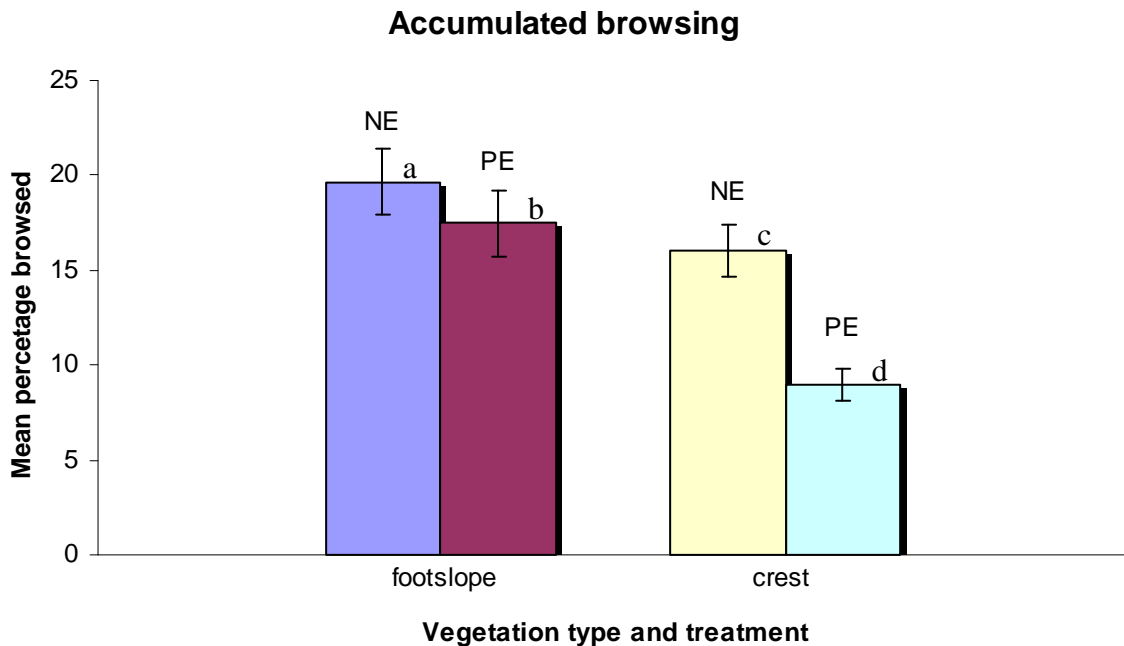


Figure 3: Accumulated browsing

Mean accumulated browsing for treatments NE and PE and both vegetation types. Percentage indicates how much of the plants above ground biomass was missing during sampling. Significant differences are indicated with different letters, and were found for comparisons between veg. types in NE and PE, and between treatments on crest and fotslope.

Throughout the study area there were individuals on which browsing was estimated to 0 %. For the fotslope vegetation the unbrowsed individuals made up approximately 6 % of the total number of individuals in NE and about 22 % in PE. For the crest vegetation the two treatments were almost the same, PE had 30 percent unbrowsed and NE had 33.

A. exuvialis was slightly more browsed than *A. grandicornuta* in both treatments (NE: 14,3 % and 16,6 %; PE 9,6 % and 11,9 %), but these differences were not statistically significant (Wilcoxon $p > 0,05$).

3.3 INDUCED RESPONSES

The two studied species had similar responses in most traits, but the treatment effect was generally stronger for *A. exuvialis*.

3.3.1 SPINE LENGTH

The measurements of spines on the first day were incorrectly performed and had to be removed from the dataset to avoid an overestimation of spine length on the footslope in FE. In total there were 2636 spines measured on *A. exuvialis*, with a mean length of 5,2 mm (Figure 4). *A. grandicornuta* had 2408 spines measured, with a mean length of 5,5 mm. For *A. exuvialis* the spines in FE were significantly shorter than those in both NE (Wilcoxon $p < 0,0001$) and PE (Wilcoxon $p < 0,0001$), but no significant differences were found for *A. grandicornuta*. (Wilcoxon $p > 0,0125$).

3.3.2 SPINE ABUNDANCE

The number of spines on each shoot varied widely, but both species had an average of 14 spines per shoot. For *A. exuvialis* the number of spines on the shoots were significantly

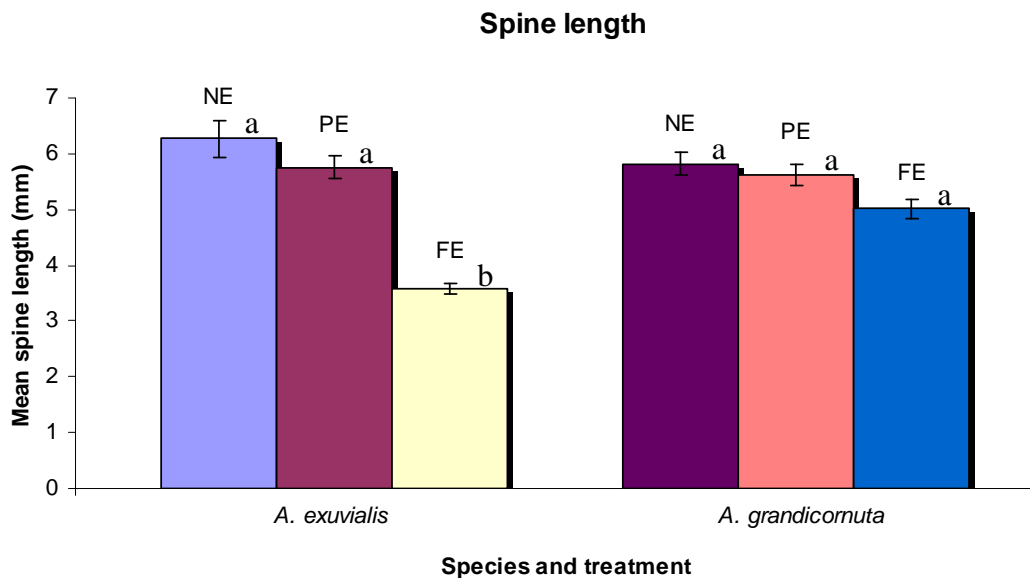


Figure 4: Spine length

Mean spine lengths for all three treatments and both species of Acacia. Significant differences are indicated with different letters, and were found for *A. exuvialis* when comparing FE with treatments open to herbivores, but not for *A. grandicornuta*.

higher in PE than in FE (Wilcoxon $p < 0,0001$), and NE (Wilcoxon $p = 0,0079$) (Figure 5). NE had significantly greater abundances than FE (Wilcoxon $p < 0,0001$). The patterns for *A. grandicornuta* were the same as for *A. exuvialis*, but with smaller non significant differences (Wilcoxon $p > 0.125$). The linear regression between spine abundance and shoot length showed a strong positive correlation with an R^2 -value of 0,67 ($p < 0,0001$).

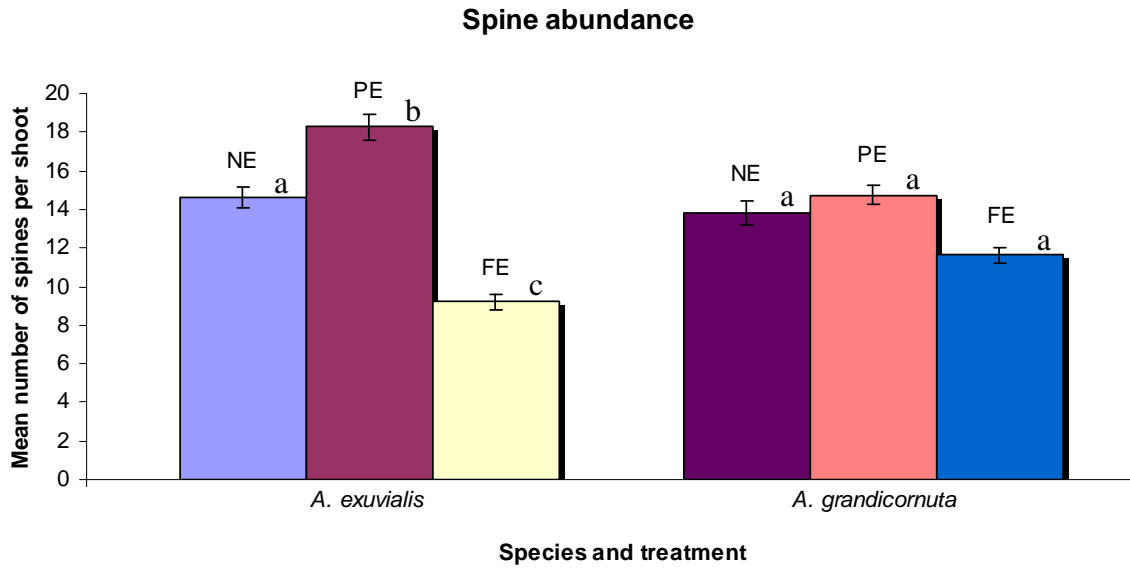


Figure 5: Spine abundance

Mean spine abundance for all three treatments and both species of Acacia. Significant differences are indicated with different letters and were found for comparisons between all treatments for *A. exuvialis* and no treatments for *A. grandicornuta*.

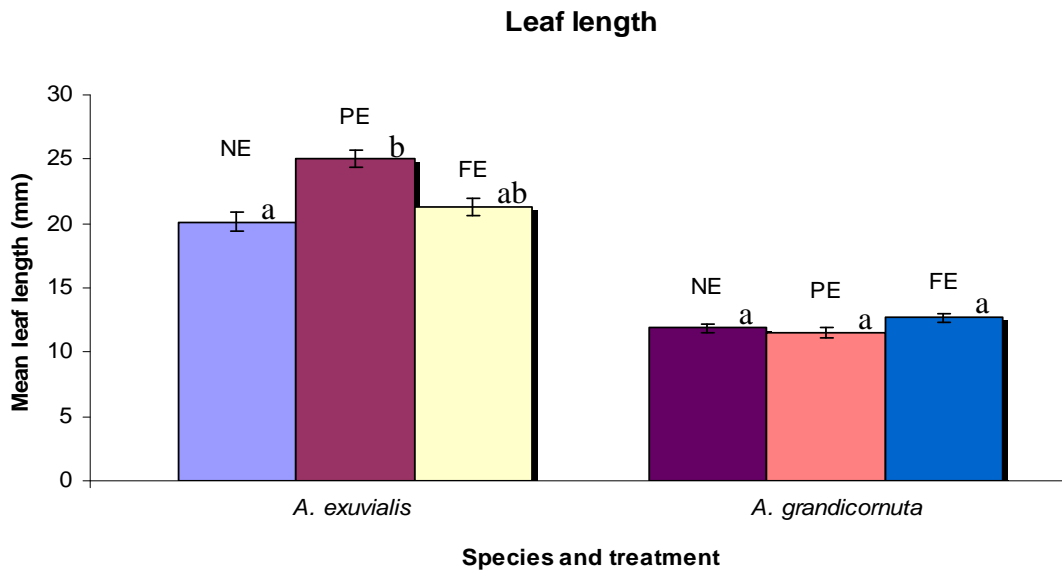


Figure 6: Leaf length

Mean leaf length for all three treatments and both species of Acacia. Significant differences are indicated with different letters and were found for *A. exuvialis* when comparing PE to NE or to FE. For *A. grandicornuta* no significant differences were found.

3.3.3 LEAF LENGTH

In total, 767 leaves were measured. The leaf lengths on *A. exuvialis* had a mean of 22,3 mm, and for *A. grandicornuta*, the mean length was 12,0 mm. The leaves of *A. exuvialis* were significantly longer in PE than in NE (Tukey HSD $p < 0,05$) but no other significant differences were found for leaf length (Tukey HSD $p > 0,05$) (Figure 6).

3.3.4 SHOOT LENGTH

Mean shoot lengths for *A. exuvialis* and *A. grandicornuta* were 50 mm and 45 mm respectively. *A. exuvialis* had significantly longer shoots in PE compared to NE and FE (Tukey HSD $p < 0,05$), and NE had longer shoots than FE (Tukey HSD $p < 0,05$) (Figure 7). For *A. grandicornuta* the relationships between treatments were the same as for *A. exuvialis* but the difference was not significant (Tukey HSD $p > 0,05$)

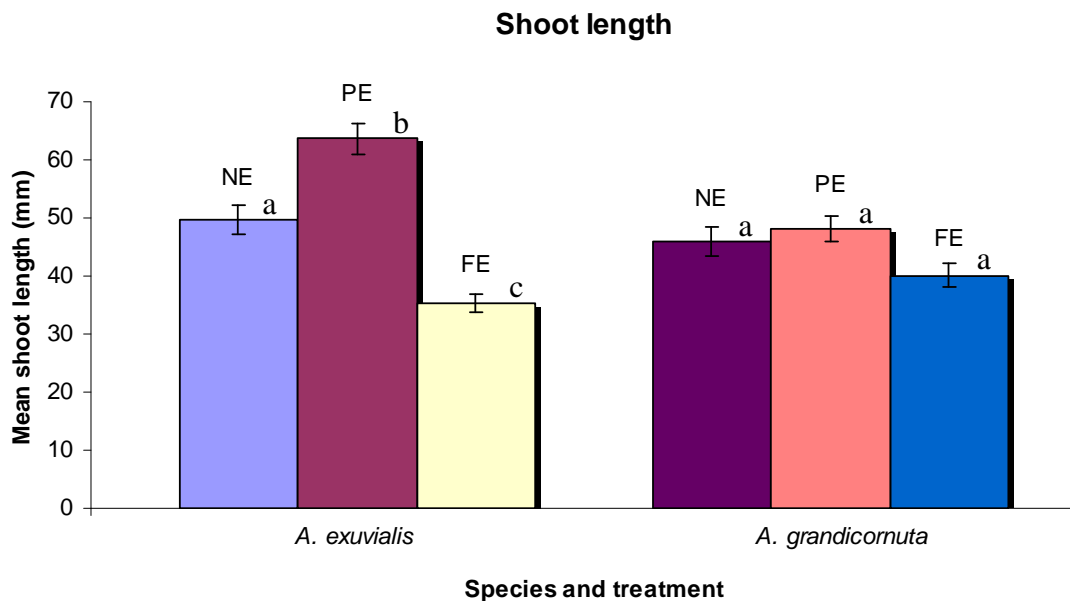


Figure 7: Shoot length

Mean shoot length for all three treatments and both species of Acacia. Significant differences were found in all comparisons between treatments for *A. exuvialis*, but only between PE and FE for *A. grandicornuta* when comparing treatments NE and PE

4. DISCUSSION

The results support hypotheses A and B, provide partial support for hypotheses C, D and F, but contradict hypothesis E.

4.1 BROWSING

I found support for hypotheses A and B. The accumulated browsing shows that the effects of herbivores were more severe in areas accessed by all herbivores than in areas where mega-herbivores were excluded. It is also apparent that the browsing was greater on the footslope vegetation than on the crest. A very interesting result is also that the effects of elephant exclusion are much greater on crest compared to footslope. The most simple explanation for the patterns in browsing pressure is that the plants in NE are browsed by a greater variety (and probably greater abundance) of mammals. The browsing of all herbivores on a plant is added together and the individuals in PE are exposed to fewer herbivores and no elephants or giraffes. Larger herbivores (such as those with access to NE) need a higher intake of nutrients (Belovsky 1986), and they eat more plant biomass than

smaller herbivores. They also have larger mouths and stronger teeth and therefore the ability to take larger bites (Belovsky et al. 1991), causing greater loss of biomass on trees in NE. When elephants feed they can also damage plants by stepping on them or simply by breaking them off to feed on branches out of their reach. This is most likely also the explanation for why more unbrowsed individuals were found in PE than in NE.

The greater effects of elephant exclusion found on crest could be due to several reasons. The woody plant species on the footslope may be more adapted to cope with the browsing than those on crest, causing a greater difference on crest when herbivores were excluded. This is quite probable, since they do experience greater browsing pressures and should adapt to them, but there is great difficulty in comparing the defences of different species to each other. There could also be some species interaction occurring on the footslope. It is possible that the presence of elephants on the footslope in NE pushes other herbivores into the footslope area of PE, and that would cause a diminished difference between the footslope areas of the two treatments. We did for instance encounter more tracks from black rhino and hippopotamus in that area than in any other area of the study site.

Effects of browsing pressure were apparent in the number of woody plants found and measured in the different parts of the study area. The lower numbers of woody individuals found on footslope were expected and quite evident when visiting the study site. These results, together with the results from browsing damage are consistent with several other studies showing greater utilization of, and greater damage to plants located near water sources (Ben-Shahar 1993, Brits et al. 2002, Calenge et al. 2002) and are likely due to congregating herbivores and greater browsing pressure near the river. The fact that the footslope of PE and NE had fewer unbrowsed individuals (Acc. Browsing = 0%) compared to the crest also supports this. Thus, the extra caution taken by game guards when escorting researchers along the river border of the exclosures is justified. The fact that more woody individuals were found in the footslope area of FE compared to the other treatments was also expected, and also shows how the herbivores affect abundances of woody plants.

But now that the herbivores have been excluded from FE for several years, shouldn't the abundance of woody plants in that treatment be the same on crest and footslope vegetation? Well, in comparison with the other treatments the difference in abundance of woody individuals is much lower in FE ($0,90 \text{ ind/m}^2$) than in NE ($2,16 \text{ ind/m}^2$) and PE ($1,97 \text{ ind/m}^2$) which could indicate that the exclusion of herbivores is causing the difference to decrease. But the exclosures have not been up long enough for the difference to disappear, and other ecological distinctions between the two types of vegetation, such as species and soil composition, will probably prevent the difference from vanishing completely.

On the crest there were more woody individuals in PE and NE than in FE, and this was not expected. There are two probable explanations for this result. First of all, the field work for this study was performed during four consecutive weeks, and sampling was spread out in the study area to reduce effects of growth on shoots, leaves and spines. During the start of the study such effects were (as far as we could see) minimal, but during the last days of field work, when sampling was carried out on the crest in PE and NE, there was some heavy rainfall which, together with beneficial weather, caused substantial sprouting by new individuals, which added some to the abundance of woody plants. This is also demonstrated by the heights of individuals found there. Only 15 % of the woody plants

found on the crest in FE were shorter than 50 cm, but for NE and PE the numbers were more than double, 37 % and 35 % respectively. But the differences in heights are also explained by damage from the herbivores in NE and PE. In 2000 a decline in tree height and the overall density of tall trees in KNP was documented by Eckhart et al. (2000) and believed to be the result of increased elephant numbers, in combination with fire. It also supports results from other studies, showing that elephants can reduce the height of browsed trees (Pellevé 1983, Baxter and Getz 2005, Makhabu 2006).

Second, the presence of large mammalian herbivores can positively influence seedling survival by suppressing populations of other smaller herbivores such as insects and rodents (Goheen et al. 2004). But why is this then not the case for the footslope vegetation also? In a study carried out at the same time as this one, Gunve (unpubl.) found that the ground cover vegetation in the study area was higher on crest than on footslope vegetation. The cover was 25 % and 40 % greater on the crest for PE and NE respectively. There is the possibility that the higher percentage of cover on the crest can provide protection and shelter for the small herbivores, which can not be offered by the footslope vegetation. Also, the ground cover increases the overall competition for nutrients, making it harder for small woody individuals to grow.

No sampling was done on browsing in FE, but the overall estimation was that the vegetation had little damage from previous browsing. However, in the study mentioned above made by Goheen et al (2004), they found that exclusion by large herbivores caused densities of rodents and insects to increase and as a result, seedling survival was greatly decreased. So even though the exclosures diminish effects from large herbivores, the possible effects of smaller ones should not be ruled out.

4.2 INDUCED RESPONSES

Results from induced response analysis provide partial support for hypotheses C, D and F, but contradict hypothesis E. The overall evidence shows that the exclusion of herbivores had an effect on spines, leaves and shoots on the Acacias. It should be said however that it is very difficult to distinguish true induced responses from indirect effects of excluded browsers, and this is further discussed below.

4.2.1 SPINE LENGTH

In accordance with hypothesis C, spine lengths were reduced when elephants and giraffes were excluded, and even more when all herbivores larger than hares were excluded. Though this effect was seen for both species of Acacia, the effect is most evident for *A. exuvialis*, where spines were 39 % shorter in FE than in NE. These results are concurrent with those found by Young et al. (2003) where spines on *A. drepanolobium* had reduced 40 % in length after 5 years of exclusion by herbivores, the same time period as in this study. The reduction of spine length with exclusion of herbivores can be explained by a relaxation in the induced defence. There is also the possibility that the reduction in spine length is not an induced response intended as a defence, but merely an indirect effect from the reduced browsing. A growing plant has a certain amount of resources to distribute among its growth points, and when one of those points is browsed, the resources will be distributed on fewer ones. So plants in the browsed areas of the study site could have longer spines because they have fewer growth points, while the individuals placed in FE have shorter spines because they distribute their resources on more points. Since growth of shoots and spines is linked, the increase in spine length in this study could simply be a result of increased shoot length. However, spine length was greatest in NE, where the browsing is most severe, and not in

PE where the shoots were longest. Thus suggesting that spine length response not only is a indirect result of a reduction in the number of growth points.

Thorns and spines have been discussed by some authors as potential “ghosts of grazing past” meaning that they are remnants from a time when they defended the plant against herbivores that are long since extinct, and not against herbivores alive today (Janzen and Martin 1981). The spines remain where the plant benefits from their presence or where very few resources are needed to produce them (Cooper et al. 2003). This is inconsistent with the results from this study where lengths and densities of spines track severity of herbivory and instead indicate that spines are more likely to be a defence against the herbivores present in the area today.

4.2.2 SPINE ABUNDANCE

The results clearly show that treatments open to all herbivores had shoots with more spines than those from which herbivores were excluded. But NE had shoots with lower abundances of spines than PE. This was a surprise and a partial disagreement with our D hypothesis, since areas with both greater proportions of browsed individuals and more severely browsed individuals were expected to have greater abundances of spines. But when comparing the results from spine abundance with those from shoot length, it is apparent that the two factors are greatly linked. Results from the linear regression analysis point to the same conclusion, that the number of spines on a shoot is very dependent on the length of the shoot. This means that the great growth due to heavy rainfall at the end of the sampling had substantial effects on the undeveloped spines, and as a result the number of spines longer than 2 mm increased and we counted more of them.

An increase in the density of spines has by some authors been considered a possible reversion to juvenile growth patterns, and there is evidence that young trees are more defended than old ones (Rhoner and Ward 1997, Rooke et al. 2004). So could it be that the individuals of PE and NE in this study are being pushed back into juvenile growth form with a higher level of defence. The fact that there are very few tall individuals on the footslope in PE and NE indicates that many of the plants are definitely being held at a low height, although height in this case is a poor indicator of plant age or maturity. Very recently sprouted individuals in the study area had a more erect form than severely browsed older individuals of the same height. A more reliable distinction is that a juvenile plant does not reproduce, while a young or mature one does (Gatsuk et al. 1980). During the fieldwork it was evident that some plants held at a low height by browsing did not reproduce, even though they had clearly reached an age in which they would if they were not as heavily browsed. So it is possible that this theory is applicable here, but with the data we have we are in no position to confirm or dismiss this hypothesis

4.2.3 LEAF LENGTH

The results from leaf length analysis contradict hypothesis E. The longest leaves were not found in NE but in PE. However, this result can probably be explained by the rapid growth near the end of field work mentioned above. PE had the longest leaves for *A. exuvialis* because more time had passed after the rain in PE than in NE, allowing leaves to grow longer. If the heavy growth had not occurred the results for *exuvialis* would probably have been the same as for *A. grandicornuta*, with FE having the longest leaves. Belovsky et al. (1991) discuss two explanations for why leaves would be shorter on plants exposed to browsing compared to those which are not; There might be nutrient and/or energy costs associated with producing longer spines, which means the plants do not have enough

resources to invest in leaves. Or the smaller leaves are part of the defence, and their relative size to the spines makes it harder for herbivores to feed on them, and as a result they choose to feed on other plants because they can't feed enough during a certain time-period. Results from shoot length analysis support the second theory. Shoot lengths were greatest in the treatments exposed to browsers, which indicates that there was no great shortage of resources for the plants there. Thus, the leaves in those treatments may have been shorter as a defence strategy (i.e. better protected by spines) and not as a result of resource restriction. Small leaves and large densities of spines is also an indication of evolution in presence of high browsing pressure from large mammals (Massei et al. 2000), which most likely is the case in Kruger.

4.2.4 SHOOT LENGTH

The patterns in shoot length partly support hypothesis F with shortest shoot lengths for FE, but longest in PE. We had expected the shoot lengths to be longest in NE because the most compensatory growth from browsing would occur there. Shoot lengths showed a very similar pattern to that of spine abundance, with greatest lengths in PE and smallest in FE. The most probable explanation for these results is the great growth at the end in PE and not a treatment effect. But the growth can not have had any effect on shoot lengths of *A. grandicornuta* since the sampling there was carried out before the rain induced growth took place. This means that the shoots being shortest in FE is probably an accurate result and an effect of resource distribution over a greater number of growth points compared to the more browsed areas.

5. CONCLUSIONS

The greater browsing pressure suffered by plants exposed to elephants and giraffes is alarming when considering the rapidly growing populations of elephants in South Africa. The growth of these populations could cause heavy damage to parts of the ecosystem, and plant response in the form of longer spines and shorter leaves makes plants less palatable. These effects are very important to consider in the widespread and growing utilization of savanna vegetation as food for livestock, because if the sizes of elephant populations continue to increase, the competition for the savanna ecosystem will do the same. The greater effects of elephant exclusion on the crest is also something that needs to be considered in the management of wild elephant populations today. The fact that different types of vegetation are affected differently by the presence/absence of elephants can be incorporated into, and assist management plans of the savanna ecosystem. But it is important to understand that even though the exclusion of elephants may decrease the browsing damage on woody plants, the herbivory is only one factor. When elephants are excluded the importance of other factors may increase, such as competition between plants, effects of smaller herbivores, decomposition or the nutrient cycle.

On February 25 2008 (during the writing of this report), SANParks decided to lift the prohibition on elephant culling as an effort to cope with the growing populations (Rodrigues 2008). It will be very interesting to see how the situation in KNP develops in the close and distant future.

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7. REFERENCES

- Augustine, D., J. and McNaughton, S., J. 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology*. 41: 45-48.
- Baxter P., W., J. and Getz W., M. 2005. A model-framed evaluation of elephant effects on tree and fire dynamics in African savannas. 15,4: 1331-1341.
- Ben-Shahar, R. 1993. Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation*. 65,3: 249-256.
- Belovsky, G., E. 1986. Generalist herbivore foraging and its role in competitive interactions. *American Zoologist*. 26: 51-69.
- Belovsky, G., E., Schmitz, O., J., Slade, J., B. and Dawson T., J. 1991. Effects of spines and thorns on Australian arid zone herbivores of different body masses. *Oecologia*. 88: 521-528.
- Blanc, J., J., Barnes, R., F., V., Craig, G., C., Dublin, H., T., Thouless, C., R., Douglas-Hamilton, I. and Hart, J., A. 2007. African elephant status report 2007, an update from the African elephant database. Occasional paper of the IUCN species survival commission no 33.
- Boege, K. and Marquis, R., J. 2005. Facing herbivory as you grow up: the ontogeny of resistance in plants. *Trends in Ecology and Evolution*. 20,8: 441-448.
- Bossen, B. 1998. Research on African elephants *Loxodonta Africana* (Blumenbach 1797): a bibliography. *African Journal of Ecology*. 36: 371-376.
- Botes, A., McGeoch, M., A. and van Rensburg, B., J. 2006. Elephant- and human-induced changes to dung beetle (*Coleoptera: Scarabaeidae*) assemblages in the Maputaland Centre of Endemism. *Biological Conservation*. 130,4: 573-583.
- Brits, J., van Rooyen, M., W. and van Rooyen, N. 2002. Ecological impact of large herbivores on the woody vegetation at selected watering points on the eastern basaltic soils in the Kruger National Park. *African Journal of Ecology*. 40: 53-60.
- Cadman, M. 2005. The debate on elephant culling in South Africa – An overview. IFAW (International Fund for Animal Welfare). 24 pages.
- Campbell, B., M. 1986. Plant spinescence and herbivory in a nutrient poor ecosystem. *Oikos*. 47: 168-172.
- Calenge, C., Maillard, D., Gaillard, JM., Merlot, L. and Peltier, R. 2002. Elephant damage to trees of wooded savanna in Zakouma national park, Chad. *Journal of Tropical Ecology*. 18: 599-614.
- Cash, V., W. and Fulbright, W., E. 2005. Nutrient enrichment, tannins and thorns: Effects on browsing of shrub seedlings. *Journal of Wildlife Management*. 69,2: 782-793.

- Cooper, S., M. and Owen-Smith, N. 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia*. 68: 446-455.
- Cooper, S., M., Owens, M., K., Spalinger, D., E. and Ginnett, T., F. 2003. The architecture of shrubs after defoliation and the subsequent feeding behaviour of browsers. *Oikos*. 100: 387-393.
- Cumming, D., H., M., Fenton, M., B., Rautenbach, I., L., Taylor, R., D., Cumming, G., S., Cumming, M., S., Dunlop, J., M., Ford, A., G., Hovoka, M., D., Johnston, D., S., Kalkounis, M., Mahlangu, Z. and Portfors, C., V., R. 1997. Elephants, woodlands and biodiversity in Southern Africa. *South African Journal of Science*. 93,5: 231-236.
- Danell, K., Bergström, R. and Edenius, L. 1994. Effects of large mammalian browsers on architecture, biomass and nutrients of woody plants. *Journal of Mammalogy*. 75: 833-844.
- Dangerfield, J., M. and Modukanele, B. 1996. Overcompensation by *Acacia erubescens* in response to simulated browsing. *Journal of Tropical Ecology*. 12,6: 905-908.
- Du Toit, J., T., Bryant, J., P. and Frisby, K. 1990. Regrowth and Palatability of *Acacia* Shoots Following Pruning by African Savanna Browsers. *Ecology*. 71,1: 149-154.
- Eckhart, H., C., van Wilgen, B., W and Biggs, H., C. 2000. Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *African Journal of Ecology*. 38: 108-115.
- Fenton, M., B., Cumming, D., H., M., Rautebach, I., L., Cumming, G., S., Cumming, M., S., Ford, G., Taylor, R., D., Dunlop, J., Hovoka, M., D., Johnston, D., S., Portfors, C., V., Kalounis, M., C. and Mahlangu, Z. 1998. Bats and the loss of tree canopy in African woodlands. *Conservation Biology*. 12,2: 399-407.
- Gadd, M., E., Young, T., P. and Palmer, T., M. 2001. Effects of simulated shoot and leaf herbivory on vegetative growth and plant defense in *Acacia drepanolobium*. *Oikos*. 92: 515-521.,2: 675-696.
- Gatsuk, L., E., Smirnova, O., V., Vorontzova, L., I., Zaugolnova, L., B. and Zhukova, L., A. 1980. Age states of plants of various growth forms: A review. *The Journal of Ecology*. 68,2: 675-696.
- Goheen, J., R., Keesing, F., Allan, B., F., Ogada, D. and Ostfield, R., S. 2004. Net effects of large mammals on *Acacia* seedling survival in an African savanna. *Ecology*. 85,6: 1555-1561.
- Goheen, J., R., Young, T., P., Keesing, F. and Palmer, T., M. 2007. Consequences of herbivory by native ungulates for the reproduction of a savanna tree. *Journal of Ecology*. 95: 129-138.
- Grubb, P., J. 1992. A positive distrust in simplicity – lessons from plant defences and from competition among plants and among animals. *Journal of Ecology*. 80 585-610.
- Gunve, E. Not published. Master thesis on vegetation in Kruger National Park.
- Hanley, M., E., Lamont, B., B., Fairbanks, M., M. and Rafferty, C., M. 2007. Plant structural traits and their role in anti-herbivore defences. *Perspectives in Plant Ecology, Evolution and Systematics*. 8,4: 157-178.
- Herms, D., A. and Mattson, W., J. 1992. The dilemma of plants: To grow or defend. *The Quarterly Review of Biology*. 67: 283-335.
- Hjältén, J., Danell, K. and Ericson, L. 1993. Effects of simulated herbivory and intraspecific competition on the compensatory ability of birches. *Ecology*. 74: 1136-1142.
- Janzen, D., H. and Martin, P., S. 1982. Neotropical anachronisms: The Fruit the *Gomphotheres* Ate. *Science*. 215,4528: 19-27.

- Lombard, A., T., Johnson, C., F., Cowling, R., M. and Pressey, R., L. 2001. Protecting plants from elephants: botanical reserve scenarios within the Addo Elephant National Park, South Africa. *Biological Conservation*. 102: 191-203.
- Maschinski, J. and Whitham, T., G. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *The American Naturalist*. 134: 1-19.
- Makhabu, S., W., Skarpe, C. and Hytteborn, H. 2006. Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers. *Acta Oecologica*. 30: 136-146.
- Massei, G., Hartley, S., E. and Bacon, P., J. 2000. Chemical and morphological variation of Mediterranean woody evergreen species: Do plants respond to ungulate browsing? *Journal of Vegetation Science*. 11,1: 1-8.
- Midgley, J.J. and Bond, W.J. 2001. A synthesis of the demography of african acacias. *Journal of Tropical Ecology*. 17: 871-886.
- Milewski, A., V., Young, T., P. and Madden, D. 1991. Thorns as induced defences: experimental evidence. *Oecologica*. 86: 70-75.
- Moolman, H., J., and Cowling, R., M. 1994. The impact of elephant and goat grazing on the endemic flora of South Africa succulent thicket. *Biological conservation*. 68,1: 53-61.
- Moorby, J and Wareing, F. 1963. Ageing in woody plants. *Annals of Botany*. 37,106: 291-308.
- Obeso, J., R. 1997. The induction of spinescence in European holly leaves by browsing ungulates. *Plant Ecology*. 129: 149-156.
- Ohgushi, T. 2005. Indirect interaction webs: Herbivore-induced effects through trait change in plants. *Annual Review of Ecology, Evolution and Systematics*. 36: 81-105.
- O'Keefe, T. and Alard, G. 2002. Effects of herbivores and fire on riparian and upland savanna ecosystems. *Field Operations Manual for Herbivore and Fire Exlosures on the Sabie and Letaba Rivers in the Kruger National Park*.
- Owen-Smith, N. 1988. *Megaherbivores: The influence of very large body size on ecology*. Cambridge University Press, Cambridge.
- Pellew, R., A., P. 1983. The impacts of elephant, giraffe and fire on upon the *Acacia tortilis* woodlands of the Serengeti. *African Journal of Ecology*. Nairobi. 21,1: 41-74.
- Rhoner, C. and Ward, D. 1997. Chemical and mechanical defense against herbivory in two sympatric species of desert Acacia. *Journal of Vegetation Science*. 8: 717-726.
- Rodrigues, J. 2008. Too hungry, too destructive, too many: South Africa to begin elephant cull. *The Guardian*. <http://www.guardian.co.uk/environment/2008/feb/26/environment> Tuesday February 26.
- Rooke, T., Danell, K., Bergström, R., Skarpe, C. and Hjältén, J. 2004. Defensive traits of savanna trees – the role of shoot exposure to browsers. *Oikos*. 107: 161-171.
- SAS Institute, 20007. *JMP User Manual*.
- Schimdt, E., Lötter, M. and McClelland, W. 2007. *Trees and shrubs of Mpumalanga and Kruger National Park*. Jacana. 702 pages.
- Smit, I., P., J., Gran, C., C. and Devereux, B., J. 2007. Do artificial waterholes influence the way herbivores use the lanscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*. 136: 85-99.
- Smit, G.N. 2004. An approach to tree thinning to structure southern African savannas for long-term restoration from bush encroachment. *Journal of Environmental Management* 71: 179-191.
- Strauss, S., Y. and Agrawal, A., A. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution*. 14,5: 179-185.

- Styles, C., V. and Skinner, J., D. 2000. The influence of large mammalian herbivores on growth form and utilization of mopane trees, *Colophospermum mopane*, in Botswana's Northern Tuli Game Reserve. *African Journal of Ecology*. 38: 95-101.
- Whyte, I. 2005. Ecosystem resources influencing elephant populations. History of the KNP elephant population. In: *Elephant effects on biodiversity; An assessment of current knowledge and understanding as basis for elephant management in SANParks*.
- Wilson, S., L. and Kerley, G., I., H. 2003. The effect of plant spinescence on the foraging efficiency of bushbuck and boergoats: browsers of similar body size. *Journal of Arid Environments*. 55: 150-158.
- Young, T., P. 1987. Increased thorn length in *Acacia drepanolobium* – an induced response to browsing. *Oecologica*. 71: 436-438.
- Young, T., P. and Okello, B., D. 1998. Relaxation of induced defense after exclusion of herbivores: spines on *Acacia drepanolobium*. *Oecologica*. 115: 508-513.
- Young, T., P., Stanton, M., L. and Christian C., E. 2003. Effects of natural and simulated herbivory on spine lengths of *Acacia drepanolobium* in Kenya. *Oikos*. 101,1: 171-179.