

Bush Encroachment and Herbivore Distribution in the Namibian Thornbush Savanna

by

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1. ABSTRACT

Bush encroachment is a phenomenon that occurs in savanna regions worldwide. It is characterized by the increase of biomass and abundance of woody plant species, accompanied by the suppression of perennial grasses and herbs. Bush encroachment is mainly ascribed to poor management of farmland, including overgrazing, the suppression of fires and the absence of browsers. Encroaching plant species are often unpalatable to grazers and domestic animals due to chemical and physical defenses, leading to a decreased livestock carrying capacity in the affected areas. This is especially problematic in countries like Namibia, where livestock keeping is a major source of income for both commercial and communal farmers. Although numerous models try to explain the occurrence of bush encroachment, there is agreement that herbivore impact is a central factor. Knowledge about plant-herbivore interactions, feeding preferences and habitat use of herbivores is thus crucial to develop sustainable land management systems.

This study aims to explore the interactions between woody encroachment and herbivory in the central Namibian thornbush savanna. Vegetation and herbivore distribution on the farm Erichsfelde was assessed during the dry season 2013. One of the study sites is an established longtime monitoring observatory; therefore vegetation monitoring data from 2004 to 2009 were available. Diet composition of cattle, oryx, greater kudu, and warthog was analyzed. No increase in thorn shrub cover was observed over the last decade. Locally, high densities of juvenile acacias indicated potential future encroachment. The results suggest that the current management practices on the farm support a stable state and prevent encroachment. Habitat use of wild herbivores was not dependent on grass cover or thorn shrub cover, and was thus ascribed to large-scale factors and structural diversity. Diet composition was analyzed from feces and stomach content, with deviating results between the two methods. Results of these analyses are discussed for single herbivore species.

2. ZUSAMMENFASSUNG

Savannengebiete weltweit sind von Verbuschung (englisch *bush encroachment*) betroffen. Bei diesem Prozess nehmen Biomasse und Individuenzahlen von Bäumen und Sträuchern zu, während ausdauernde Gräser und Kräuter abnehmen. Viele dieser Gehölzarten verfügen über mechanische und chemische Abwehrmechanismen und werden daher vom Vieh gemieden, was eine abnehmende Tragfähigkeit der betroffenen Gebiete zur Folge hat. Verbuschung wird hauptsächlich auf ein mangelhaftes Landmanagement zurückgeführt, insbesondere auf Überweidung sowie den Ausschluss von Feuern und äsenden Herbivoren.

In Namibia, wo ein großer Teil der Bevölkerung seine Einnahmen aus der kommerziellen oder kommunalen Viehzucht bezieht, ist dies besonders problematisch. Eine Vielzahl von Modellen versucht, die Ursachen der Verbuschung zu beschreiben. Herbivorie wird dabei häufig als zentrales Element gesehen. Kenntnis über Tier-Pflanze-Interaktionen, Nahrungspräferenzen und Habitatnutzung von Herbivoren ist daher von großer Wichtigkeit für die Entwicklung nachhaltiger Landnutzungsstrategien.

Im Rahmen der vorliegenden Arbeit wurden die Zusammenhänge zwischen Herbivorie und Verbuschung in der zentralnamibischen Dornstrauchsavanne untersucht. Vegetation und Herbivorenverteilung auf der Farm Erichsfelde wurden während der Trockenzeit 2013 aufgenommen. Bei einem der Untersuchungsareale handelt es sich um ein Langzeit-Observatorium, so dass Vegetationsdaten aus den Jahren 2004 bis 2009 zum Vergleich vorlagen. Die Nahrungszusammensetzung von Rindern, Spießbock, Großem Kudu und Warzenschwein wurde analysiert. Während des letzten Jahrzehnts konnte keine Zunahme der Dornstrauch-Deckung nachgewiesen werden. Jedoch wurden lokal hohe Dichten von juvenilen Akazien beobachtet, die Potenzial für zukünftige Verbuschung erkennen lassen. Die Ergebnisse deuten an, dass das gegenwärtige Landmanagement der Farm der Verbuschung entgegenwirkt und ein stabiles Verhältnis von Gräsern und Sträuchern fördert. Die Habitatnutzung der Herbivoren konnte nicht durch Gras- oder Dornstrauchdeckung erklärt werden und wurde daher auf großräumige Faktoren und strukturelle Diversität zurückgeführt. Die Nahrungszusammensetzung wurde aus Faeces und Mageninhalt bestimmt, mit abweichenden Resultaten zwischen den beiden Analysen. Die Ergebnisse werden für die einzelnen Arten diskutiert.

3. INTRODUCTION

Savanna ecosystems cover large proportions of Africa, Australia, South America and Asia, in total about an eighth of the global land surface (Scholes & Archer 1997). They contain the majority of the world's rangeland and livestock, supporting the livelihood of a large percentage of the human population (Scholes & Archer 1997). Degradation of rangeland is thus a major problem.

A phenomenon that occurs worldwide in savanna regions is bush encroachment, i.e. the increase of biomass and abundance of woody plant species, accompanied by the suppression of perennial grasses and herbs (Ward 2005, O'Connor et al. 2014). Encroaching plant species are often unpalatable to grazers and domestic animals due to chemical and physical defenses (Rohner & Ward 1997, Ward 2005). This leads to a decreased livestock carrying capacity in the affected areas and can create economic loss (Bester & Reed 1997, Lange et al. 1998). Bush encroachment is mainly ascribed to poor management of farmland, including overgrazing (van Vegten 1983, Skarpe 1990b, Scholes & Archer 1997, Lange et al. 1998), the suppression of fires (Scholes & Archer 1997, de Klerk 2004) and the absence of browsers (Scholes & Archer 1997, Smit et al. 1999). Often countermeasures are applied to control the amount of woody vegetation. These practices include mechanical control by cutting, chemical control by herbicides, and the use of fire and herbivory by browsers (Smit et al. 1999, van Rooyen 2010).

The causes of bush encroachment are complex, and numerous models have been developed to explain the interaction of grasses and trees in savanna systems. Overgrazing, lack of fire events and soil water availability are widely accepted as main drivers, although other factors like climate change and increased CO₂-levels have been discussed as possible causes (Walter 1954, Archer et al. 1995, Scholes & Archer 1997, Smit et al. 1999, Ward 2005, Bond 2008.). In the classical two-layer model of Walter, niche separation between grasses and trees is a key element in savanna systems (Walter 1971, cited in Scholes & Archer 1997). Grasses are very efficient in water uptake from the upper soil layers due to their intensive root system and outcompete woody plants for water in the topsoil. Deep-rooted woody plants on the other hand can exclusively access subsoil water (Walter 1954, Walter & Volk 1954, Scholes & Archer 1997, House et al. 2003). Topsoil can be regarded as the upper 30 cm of the soil, while subsoil refers to a depth of 30-130 cm (Knoop & Walker 1985). The result of this resource separation is a competitive equilibrium (van Rooyen 2010).

Walker & Noy-Meir (1982) demonstrated that under certain conditions such stable coexistence is possible. When the grass layer is damaged, e.g. by overgrazing, more water is available to support the growth of trees and shrubs. Although the model is often regarded as a simplification, it is still valuable when it comes to the general pattern of coexistence (Skarpe 1990a, Scholes & Archer 1997, Graz 2008, Ward et al. 2013).

An alternative equilibrium model is the balanced competition concept. According to this model, intraspecific competition for resources is more important than niche separation between grasses and woody plants (Scholes & Archer 1997, House et al. 2003). The more competitive species will increase in density until it is self-limited by intraspecific competition (Scholes & Archer 1997). Coexistence of grasses and trees is achieved when this self-limited density is sufficiently low and still allows the growth of less competitive species (House et al. 2003).

Non-equilibrium theories on the other hand hypothesize that there is no single equilibrium. There is no classical succession state but rather several possible states, depending on the environmental conditions. Rangeland dynamics can be described as set of discrete vegetation states (Westoby et al. 1989, Dougill et al. 1999). Transitions between those states are triggered by disturbance events, either naturally (fire, weather) or by human impact and management (e.g. stocking rate, burning, and bush clearing). Fire events and herbivory can prevent seedlings and saplings from growing above the herbaceous layer, where they are in direct competition with grasses for resources (Scholes & Archer 1997, Bond 2008). Fire events require a sufficient amount of inflammable biomass provided by the grass layer. Overgrazing reduces this fuel load and thus prevents fires (Graz 2008, O'Connor et al. 2014). Also intense herbivory itself can keep saplings within the herbaceous layer (Scholes & Archer 1997, Bond 2008). Another example is the recruitment of *Acacia mellifera*, which needs at least three years of sufficiently high rainfall in a row for successful germination and establishment of seedlings (Joubert et al. 2008). Depending on the particular cause, transitions may take place quickly or over an extended time period (Westoby et al. 1989). Small patches in different transition states between grasslands and woody dominance occur, while still the savanna can be seen as stable at a landscape scale (Scholes & Archer 1997, Dougill et al. 1999, Wiegand et al. 2005, Britz & Ward 2007). This suggests that bush encroachment could be a natural phenomenon in savanna ecosystems (Wiegand et al. 2005, Britz & Ward 2007). According to these “state-and-transition” models, certain environmental conditions or a

corresponding management should be able to favor the grass-dominated state (de Klerk 2004, Joubert et al. 2008).

Recently, the rising CO₂-level caused by global consumption of fossil fuels has been discussed as additional driver for bush encroachment (Polley et al. 1992, Archer et al. 1995, Bond 2008, Rohde & Hoffman 2012, Russel & Ward 2014). The herbaceous layer of savannas is dominated by C₄ grasses, while shrubs and trees use the C₃ photosynthetic pathway. In contrast to C₄ plants, C₃ plants close their stomata under high temperatures and dry conditions to minimize evaporation and are thus less efficient in hot arid regions. The rising atmospheric CO₂ level, caused by global change, minimizes the advantage that C₄ grasses have over C₃ trees, because it enables the latter to absorb more CO₂ while their stomata are open. CO₂ fertilization can thus favor the growth of trees and shrubs (Bond 2008, Russel & Ward 2014). Additionally, increasing CO₂ could reduce transpiration, so that more water would infiltrate the subsoil and be available for shrubs and trees (Polley et al. 1992, Bond 2008).

Inconsistencies between studies in different savanna systems suggest that the extent to which single factors impact the grass-tree ratio is highly variable, depending on the environmental conditions and the assessed spatial and temporal scales (Scholes & Archer 1997, Smit et al. 1999, House et al. 2003, de Klerk 2004). There is agreement, however, that herbivore impact is a crucial factor in savanna systems, and overgrazing by livestock is considered one of the most important drivers of bush encroachment.

Herbivores influence vegetation by the consumption of food plants, trampling, and the depositing of nutrients via feces and urine (Skarpe 1991). The habitat selection of herbivores depends amongst others on habitat structure and forage availability (Dörgeleh 2001). Food choice is influenced by the seasonal and spatial availability of forage plants and by nutritional requirements that vary between species, but also between sexes and life stages (Skarpe 1991, Staver et al 2009). Plants can react to herbivory through chemical and physical defenses (Skarpe 1991), that vice versa influence food choice. Indigenous herbivores are well adapted to their specific habitats and can response flexibly to changes in forage quality and availability. Domestic livestock in contrast is often kept in high densities, restricted in mobility, and thus limited in forage selectivity (Skarpe 1992). In addition, the presence of herbivores can alter plant species composition as palatable species will be (over)utilized while other species will be avoided and thus can increase in frequency (Skarpe 1992).

Keeping of browsing game species has already proved to be a useful after-care method to keep shrub numbers low after clearing actions and can be used to suppress the recruitment of shrubs and trees (Bester & Reed 1997, Jeltsch et al. 2000, Staver et al. 2009). Still, for southern Africa little information is available about the specific interactions of herbivore species and the vegetation surrounding them. Feeding habits and habitat use often differ between seasons and specific regions and cannot be generalized (Skarpe 1991, Staver et al. 2009). Insight about plant-herbivore interactions, feeding preferences and habitat use of herbivores is thus crucial to develop sustainable land management systems.

In Namibia, livestock keeping is a major source of income for both commercial and communal farmers. Extensive livestock ranching is practiced on about three quarters of the country's area and almost half of the commercial farming area is affected by bush encroachment (Lange et al. 1998, Joubert et al. 2008). Thus, economic loss is created.

This study aims to explore the interactions between woody encroachment and herbivory in the central Namibian thorn shrub savanna. Vegetation and herbivore distribution on four sites on the farm Erichsfelde in the central highlands of Namibia was assessed during the dry season 2013. Encroaching plant species in the area include amongst others several *Acacia* species, mainly *A. mellifera* (Bester 1999, Joubert et al. 2008). One of the study sites was established as longtime monitoring observatory within the BIOTA project (Jürgens et al. 2010, Jürgens et al. 2012). Therefore vegetation monitoring data from 2004 to 2009 were available for this site. Sites were either bush cleared by cutting and burning followed by seeding of grasses or had experienced no such measures. Focus of vegetation relevés was laid on perennial grasses and thorn shrubs, i.e. several *Acacia* species (*A. hebeclada*, *A. luederitzii*, *A. mellifera*, *A. reficiens*, and *A. tortilis*) and *Dichrostachys cinerea*. These species were chosen as they were considered the most abundant and important woody species in the greater area. Habitat use of wild herbivores was estimated using pellet counts. In addition, feeding preferences of wild and domestic herbivore species (oryx, greater kudu, warthog, and cattle) were analyzed.

In order to investigate the interactions between grazing and browsing herbivores and bush encroachment, the following study questions were addressed:

- How did the observatory develop over the last decade, i.e. was there a change in grass or thorn shrub cover?
- How do grass cover and thorn shrub densities differ between the four study sites on Erichsfelde?
- Do the herbivore species have a preference for open or shrubby habitats?
- What are the preferred feeding sources of game and cattle in the study area during the dry season?

4. METHODS

4.1. Study area Erichsfelde

Erichsfelde is a private cattle farm of 13 000 hectares. It is situated in the central Namibian highland, 40 km north of Okahandja, at an altitude of approximately 1500 m asl. Rainfall in this area is highly variable with a mean annual precipitation of approximately 350 mm, most of it during the summer months September to April (Jürgens et al. 2010). The vegetation type is a thornbush savanna. Both open grassland and patches with dense, thorny shrub cover occur. Typical grasses in the area are, amongst others, *Stipagrostis uniplumis* and several *Eragrostis* species. Woody vegetation includes several *Acacia* species with *Acacia mellifera* considered as main encroacher species (Bester 1999, Jürgens et al. 2010). Beside cattle, several game species occur on the farm (e.g. springbok, greater kudu, oryx, red hartebeest, steenbok, and warthog). The farm is subdivided in camps of 500 to 1500 hectares; it is not high fenced and game is allowed to move freely between the camps. Oryx is hunted for farm requirements, including food supply for farm workers and their families, and to a minor degree for sale. As both game and cattle are kept on the farm, it is especially suitable to analyze their feeding behavior and influence on vegetation dynamics under the same environmental conditions.

A longtime biodiversity observatory was set up on Erichsfelde within the context of the research project BIOTA Southern Africa (Jürgens et al. 2010, Jürgens et al. 2012, www.biota-africa.org) and repeatedly recorded since 2001. Thus, ecological conditions on the farm are well described, including parameters such as soil, vegetation, and climate. Apart from the observatory, three additional sites were studied during the field work as listed below.

4.1.1. Former BIOTA observatory

The observatory covers an area of 1 km² (1000 m x 1000 m) and is divided into 100 1-hectare plots. These are ranked from 1 to 100 according to the habitat types they represent (for detailed information about the ranking procedure see Jürgens et al. 2012). Each of them includes a 100 m² vegetation subplot in their center. Complete vegetation relevés of the 20 highest ranked 100 m² plots exist for the years 2004 to 2009. After an interruption between 2010 and 2012, these plots were accessed again in the context of this thesis. No bush clearing measures were carried out on this site.

4.1.2. Kudu 2

This camp was bulldozer cleared and ripped (>0.5 m deep, 1 m spacing) in December 2010. Buffalo grass (*Cenchrus ciliaris*) was seeded in January 2011 (farm manager Rudi Scheidt, pers. comm.).

4.1.3. Rehab

The cleared section of Rehab camp was stump-burned in November 2010 to remove *Acacia mellifera* bushes. Dead wood was not removed, but remained on the camp. Seeds of various grass species mixed with cattle dung were brought out soon after clearing (farm manager Rudi Scheidt, pers. comm.).

4.1.4. Rehab East

This site was not bush cleared and is situated directly next to the cleared section of Rehab camp, without fences separating the two sites.

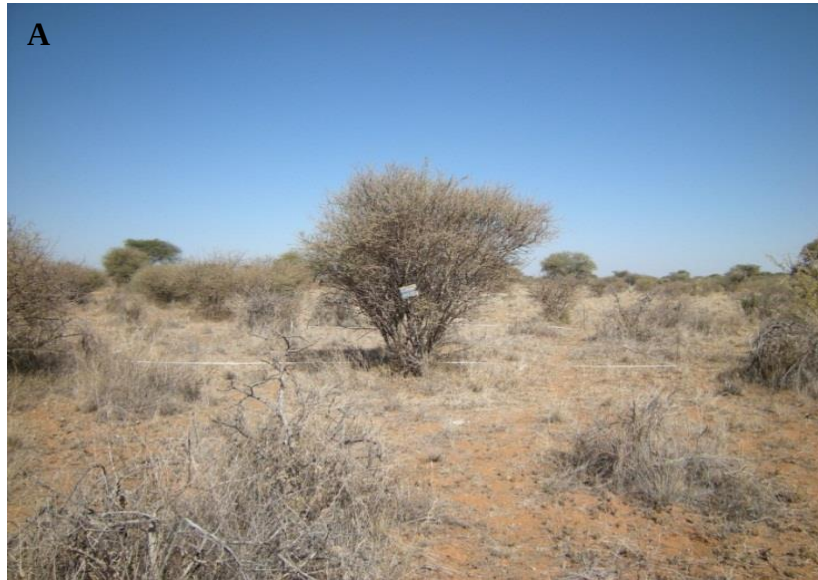


Figure 1: Study sites on Erichsfelde. A: Observatory; B: Kudu 2; C: Rehab; D: Rehab East.

4.2. Vegetation relevés

A total of 56 vegetation relevés were carried out on four study sites on Erichsfelde (Table 1). All relevés had a size of 100 m² (10 m x 10 m). Apart from the Observatory plots, which had fixed coordinates, the positions of plots were defined using random numbers. GPS coordinates were taken. The plots were marked with measuring tape and subdivided in three sections with a rope to simplify recording. Plant species within the plots were determined, with the focus put on perennial grasses and woody plants. Cover of plant species was estimated in percent. Grasses were pooled for cover estimation, because identification to species level was difficult during the dry season and total grass cover was considered to be the key factor in the balance between grasses and thorn shrubs. In the dry season, the grass layer is formed predominantly by perennial species, but also by a few remaining annual or biannual species and the term “grasses” is used here in this sense. For thorn shrubs, i.e. *Acacia* species (*A. hebeclada*, *A. luederitzii*, *A. mellifera*, *A. reficiens*, and *A. tortilis*) and *Dichrostachys cinerea*, individual numbers were recorded. These species were chosen for the study as *Acacia* species and *D. cinerea* are reported to be the most important encroachers in the area (Bester 1999, Jürgens et al. 2010).

For the Observatory plots, some inconsistencies in vegetation data from the preceding years and the data collected in this study must be considered. *Acacia luederitzii* and *Acacia reficiens* were obviously identified differently by different observers. Due to the morphological and ecological similarities of the two species, they were summarized as a single category for further data analysis. For grasses, cover values of single species were recorded during the preceding years, while in this study total cover of grasses was estimated. To compare cover values, the single covers of the previous data sets were summed up to get the total cover that is used in this study. As all grasses share the same vegetation stratum, it is assumed that the bias caused by this aggregation is small.

Table 1: Management types and number of plots at the four study sites.

	Observatory	Kudu 2	Rehab	Rehab East
Bush clearing	none	bulldozer cleared (December 2010)	stump-burned (November 2010)	none
Seeding	-	<i>Cenchrus ciliaris</i>	various grasses	-
No of relevés	20	12	12	12

4.3. Pellet counts

To estimate the habitat use of the surveyed herbivore species, walked transects were carried out at every plot. Cross-shaped transects of 2 x 100 m were used (Figure 2). Along these transects, all fresh pellet groups within 1 m to the left and the right were determined and counted. Pellets still dark in color and without signs of decomposition (e.g. by termites or dung beetles) were defined as fresh.

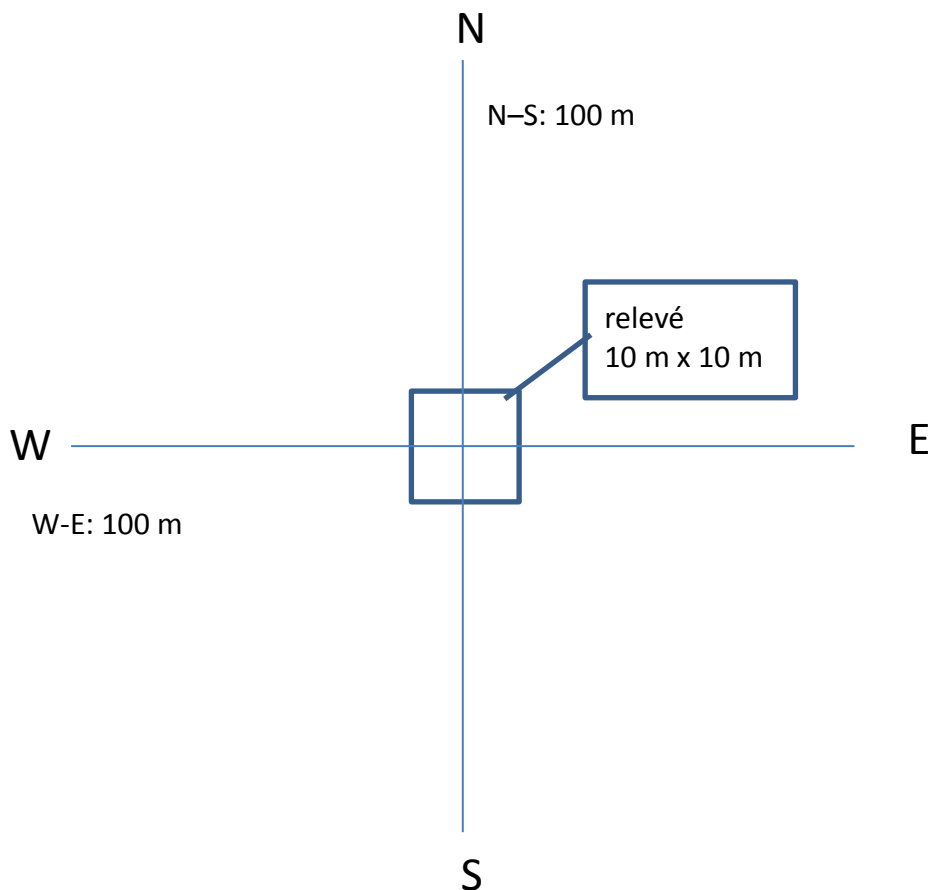


Figure 2: Position of transects in relation to vegetation relevés.

4.4. Sampling of feces

To estimate the food composition of herbivores, feces of the following species were sampled: oryx (*Oryx gazella* LINNAEUS), greater kudu (*Tragelaphus strepsiceros* PALLAS), warthog (*Phacochoerus africanus* GMELIN), and cattle (*Bos primigenius taurus* LINNAEUS). These species were chosen because of their high abundance on the farm and the easy-to-identify character of their droppings. Identification of the feces was done (a) via visual observation and (b) by shape-based determination using the “Field Guide to the Tracks & Signs of Southern, Central & East African Wildlife” (Stuart & Stuart 2013). The droppings were collected where found; salt licks turned out as good sampling places as they were frequently visited by the antelope species and fresh feces were available there. Samples were sundried and stored in paper bags.

4.5. Sampling of stomach content

As oryx is hunted on Erichsfelde, there was the opportunity to sample the rumen content of seven shot individuals. In addition, rumen content of one cow (from the neighboring farm Hüttenhain) and stomach content of one warthog were sampled as case examples. Samples were filled into 50 mL plastic tubes and preserved with alcohol until they could be properly sun dried.

4.6. Analysis of feces

4.6.1. Preparation of plant references

For reference purpose, material of the 25 most abundant plant species was chosen (Table 13, chapter 10.2.) Leaves, flowers, and stems respectively were separated and ground in a ball mill (Retsch MM 400).

A small amount of the ground plant material was brought out on microscope slides with a small scoop; some chloral hydrate solution (chloral hydrate : water : glycerin = 80 : 100 : 50) was added and the preparation was covered with a cover slip. This bleaching procedure is, in different adaptations, commonly used to process plant material for histological analysis (Gardner 1975).

The plant material was then examined under a microscope (Leica DM 5000B). A camera (Leica DFC 450) was used to take reference photographs.

4.6.2. Analysis of fecal samples

Samples were ground in a mortar, using three pellets per sample for the antelope species (oryx, kudu), two half pellets for warthog, and an equivalent amount of cattle feces. They were then sieved through a fine sieve (tea strainer) to remove coarse particles that would disturb the further analysis. Bleaching was done using chloral hydrate as described for plant reference samples. Analysis was done by counting fragments under a transmitted light microscope (Carl Zeiss KF 2) in adaptation of the method of Stewart (1967): Two parallel lines were marked on the cover slips and all fragments lying partly or entirely between that lines were counted. Per sample, three slides were counted out to a minimum of 100 fragments in total. If necessary, a fourth slide was counted. A magnification of 10 x 10 was used, switching to 40 x 10 when necessary. Fragments were determined as far as possible using the reference photographs. Keys used for analysis of monocot particles were Liversidge (1970) pp. 153-165, Kok & van der Schijff (1973) pp. 27-43 and Lensing (1979) pp. 71-122. Undetermined fragments were counted as such, except for particles smaller than two cells. Those could have been removed prior to analysis by fine sieving; this was skipped for time saving. It was shown by Dirschl (1962, cited in Lensing 1982), that sieving of rumen content with different mesh sizes does not alter the proportion of different particles. Different types of hairs (e.g. stellate hairs) were nevertheless counted, as they can provide information about monocots/dicots being present in the samples.

4.7. Analysis of stomach content

Stomach content was counted out under a stereo microscope at a magnification of 50 (microscope: Zeiss Stemi SV6, gooseneck lamp: Zeiss KL 1500 LCD). Samples were sieved through a fine sieve (tea strainer), thoroughly rinsing with water to remove slimes. Small amounts were brought out on a petri dish with a hand drawn 4 x 5 grid, the distance between the lines being 1.5 cm. The fragments on or closest to the cross points were determined as far as possible and counted. Six dishes per sample were examined, resulting in a total count of 120 particles.

4.8. Data analysis

Data were analysed using Microsoft Excel 2010 and IBM SPSS Statistics for Windows, Version 22. All data were tested for deviation from normality prior to analysis. For data deviating from normal distribution non-parametric tests were used. Where multiple post-hoc tests were necessary, the Bonferroni-Holm method was used to adjust the level of significance and to control type 1 errors.

4.8.1. Vegetation data

Complete vegetation data of the Observatory were available from 2004 to 2009 and for 2013. Data were recorded in May (2004), April (2005-2009) and May/June (2013) respectively.

Acacia luederitzii & *Acacia reficiens* and all intermediate forms between them were summarized to a single category because of their similarity and hybridization between the two species, making them almost undistinguishable under field conditions.

A hierarchical cluster analysis was done to classify the Observatory plots according to their specific proportions of grasses and thorn shrubs. Mean cover values of grasses and thorn shrubs were compared between clusters using a Mann-Whitney U test. Comparison of grass cover and thorn shrub cover between the four sites as well as analysis of thorn shrub individual numbers was done using Kruskal-Wallis tests with pairwise Mann-Whitney-U tests (Bonferroni-Holm corrected).

4.8.2. Precipitation data

Monthly precipitation sums from 2003 to 2013 were obtained from the Tropical Rainfall Measuring Mission (TRMM) and were kindly provided by V. Baumberg. For further information on TRMM see Kummerow et al. (1998), Simpson et al. (1996), and <http://trmm.gsfc.nasa.gov/>.

4.8.3. Herbivore distribution

Pellet counts from Rehab and Rehab East were analyzed using a Mann-Whitney U test. Due to the spatial proximity of the two sites only one was included in further comparisons with the Observatory and Kudu 2. For this, Rehab East was chosen as it differed more from the other study sites. Pellet count comparisons between the Observatory, Kudu 2 and Rehab East were

done using Kruskal-Wallis tests with pairwise Mann-Whitney-U tests (Bonferroni-Holm corrected).

Generalized Linear Models were carried out to test the impact of grass cover, thorn shrub cover and sites on herbivore distribution. To test for correlations in the distribution of oryx and kudu, Spearman-Rho's correlation was used.

4.8.4. Diet selection

For analysis of particle numbers in feces and stomach content, Kruskal-Wallis tests with pairwise Mann-Whitney-U tests were carried out (Bonferroni-Holm corrected).

4.8.5. Boxplots

Where boxplots (Figure 3) are used for visualization of data, the single parts of the boxplot indicate statistical parameters as follows:

- Bottom of box: first quartile (25th percentile)
- Band inside box: median (50th percentile)
- Top of box: third quartile (75th percentile)
- Ends of whiskers: minimum and maximum
- Circle: outliers greater than 1.5 interquartile ranges
- Asterisk: outliers greater than 3 interquartile ranges

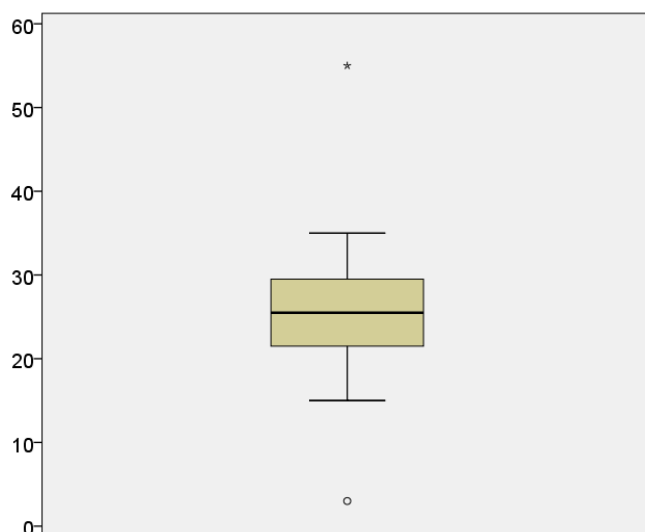


Figure 3: Example of a boxplot.

5. RESULTS

5.1. Observatory: Vegetation changes over time

5.1.1. Cover values of grasses and thorn shrubs

Grass cover and cover of thorn shrub species on the Observatory was evaluated over the last decade (Figure 4). Grass cover was highly variable during the observation period, with the lowest cover in 2007 (median 6.1 %) and the highest cover in 2006 (median 54.2 %; Kruskal-Wallis: $\chi^2=90.449$, $p<0.001$, $n=140$). Variation does not show a directional development, but seems to vary with rainfall in the actual years (Figure 5). High grass cover in 2006 coincides with a good rainy season, with a precipitation of 780 mm during the months September to April. In the following year, rainfall during the same period only added to 310 mm, resulting in a low cover of grasses. Grass cover even stays rather low during the subsequent years 2008 (470 mm) and 2009 (550 mm), although precipitation during the rainy season was higher again (Figure 4, Figure 5).

Total thorn shrub cover varied only little between years, with lowest cover in 2005 (median 4.1 %) and highest cover in 2013 (median 13.5 %; Kruskal-Wallis: $\chi^2=6.188$, $p=0.40$, $n=140$). *Acacia mellifera* constitutes the major part of these thorn shrubs, while all other species (*A. hebeclada*, *A. luederitzii/reficiens*, *A. tortilis*, and *Dichrostachys cinerea*) generally reach only cover values below 10 %. There is no trend for an increase of thorn shrub cover over time (Figure 4).

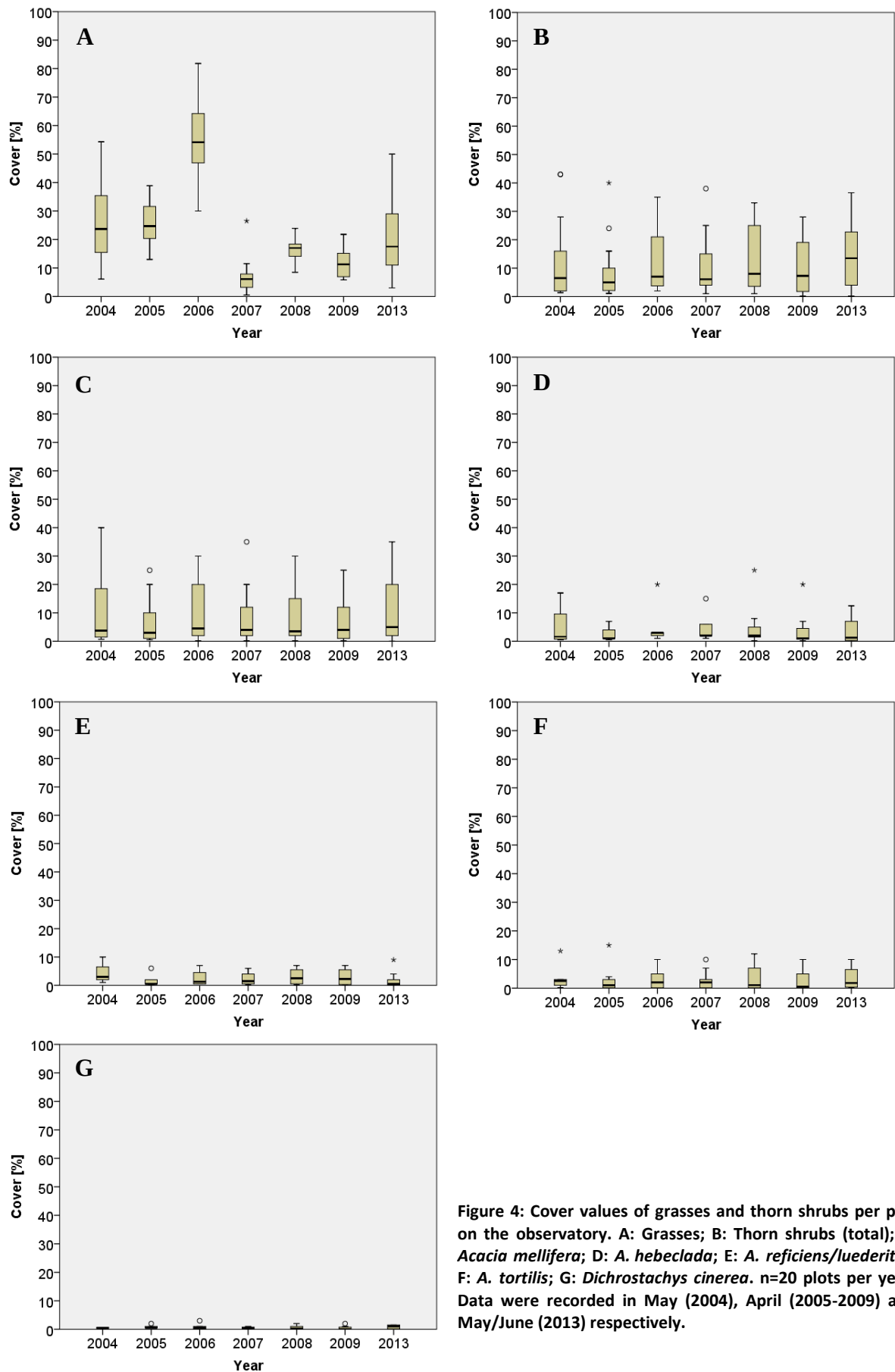


Figure 4: Cover values of grasses and thorn shrubs per plot on the observatory. A: Grasses; B: Thorn shrubs (total); C: *Acacia mellifera*; D: *A. hebeclada*; E: *A. reficiens/luederitzii*; F: *A. tortilis*; G: *Dichrostachys cinerea*. n=20 plots per year. Data were recorded in May (2004), April (2005-2009) and May/June (2013) respectively.

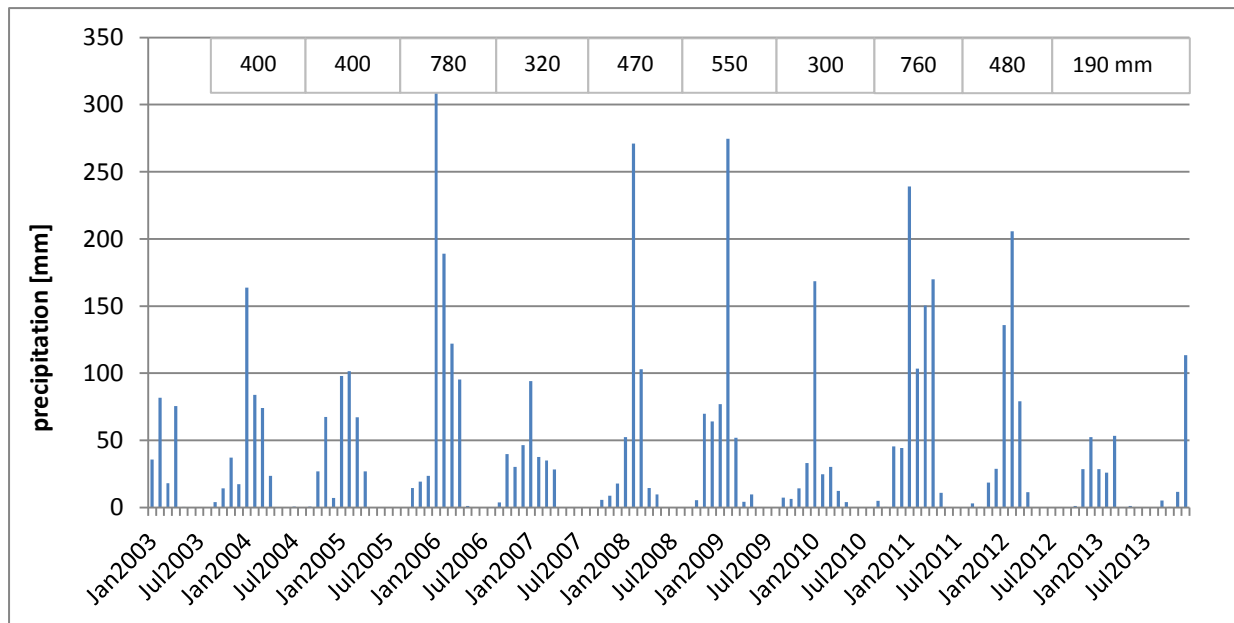


Figure 5: Monthly precipitation [mm] on the observatory Erichsfelde. Boxes at the top give precipitation sums for September to April (rounded to the nearest ten). Data provided by V. Baumberg; Data Source: TRMM.

5.1.2. Hierarchical cluster analysis

A hierarchical cluster analysis was carried out to classify the 20 Observatory plots according to their specific proportions of grasses and thorn shrubs over the years. Two clusters emerged, as shown in Figure 6. Both are similar in terms of grass cover, but differ strongly in the amount of thorn shrubs (Figure 7, Figure 8).

Cluster 1 includes 14 plots that are characterized by a persistently low thorn shrub cover throughout the years, rarely exceeding 10 %. Grass cover is fluctuating between below 10 % in 2007 and about 60 % in 2006 (Figure 7, Figure 8).

Cluster 2 includes 6 plots that are characterized by a high cover of thorn shrubs. Shrub cover ranges between approximately 15 % in 2005 and 30 % in 2006, grass cover ranges between below 10 % in 2007 and 50 % in 2006 (Figure 7, Figure 8).

Mean cover values per year of grasses and thorn shrubs were compared with a Mann-Whitney-U test. Grass cover did not differ between clusters (Mann-Whitney $U=18.0$, $z=-0.831$, $p=0.406$, $n=7$ years). Thorn shrub cover was significantly higher on cluster 2 plots (Mann-Whitney $U=0.0$, $z=-3.134$, $p=0.002$, $n=7$ years; Figure 8).

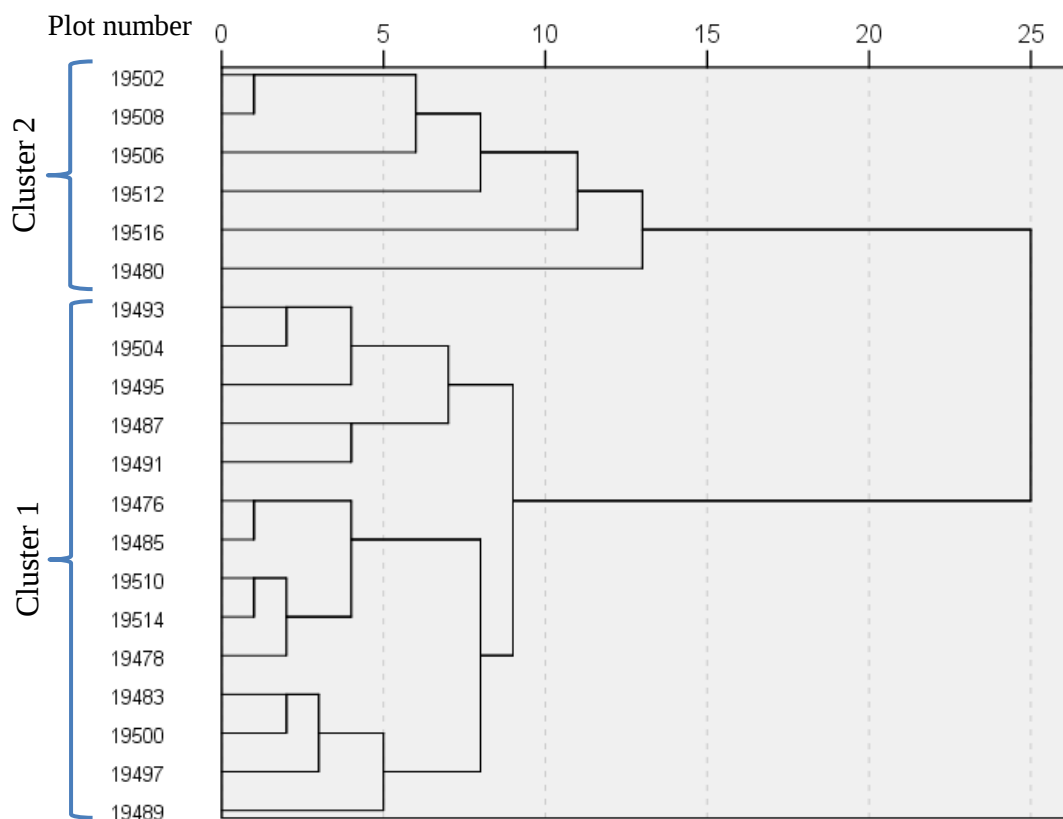


Figure 6: Dendrogram of the Observatory plots (results of hierarchical cluster analysis). n= 20 plots.

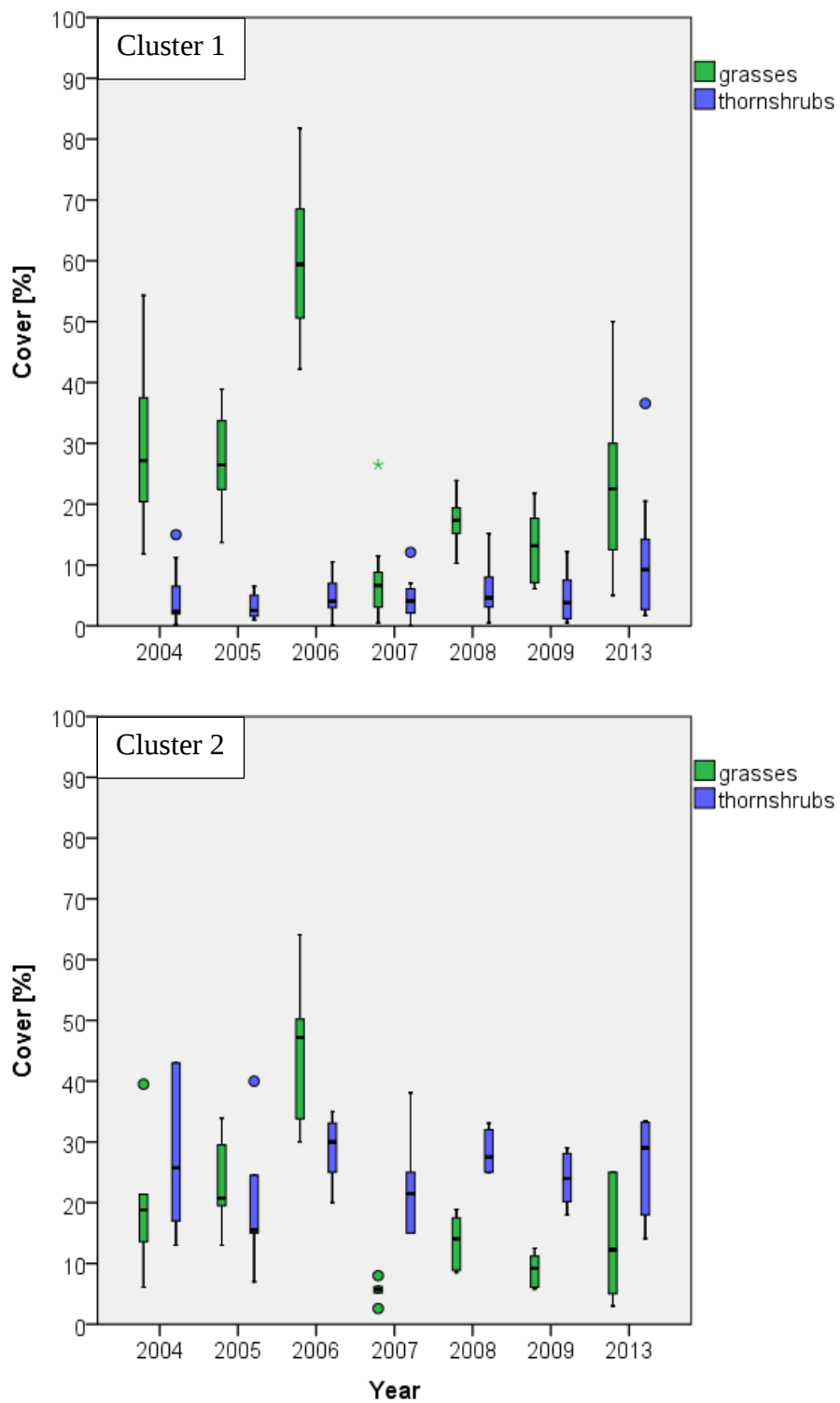


Figure 7: Cover of grasses and thorn shrubs of the vegetation clusters on the Observatory. Cluster 1: n=14 plots; Cluster 2: n=6 plots.

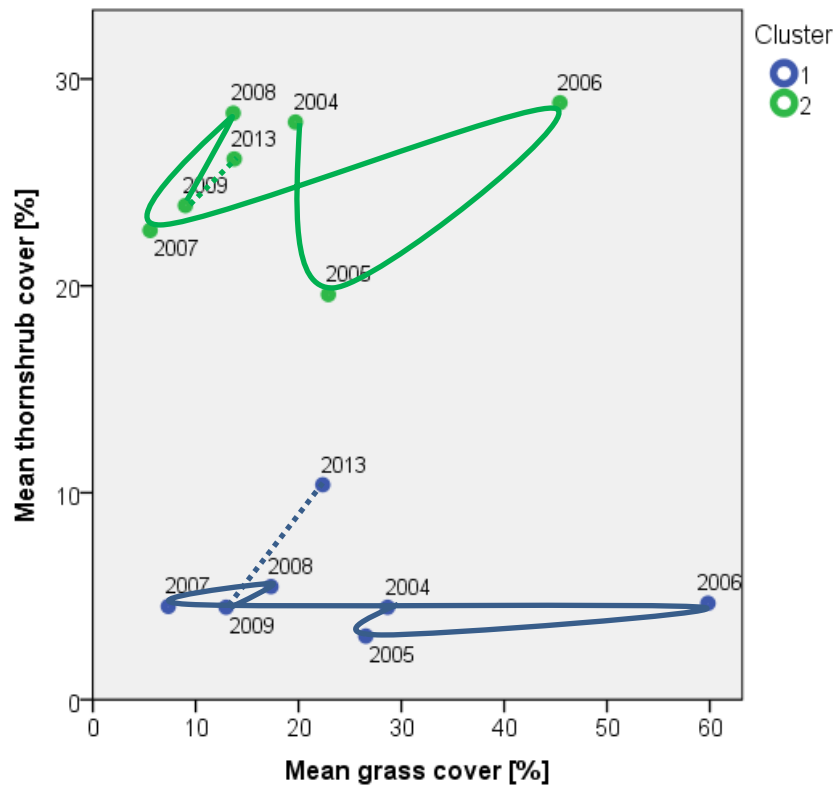


Figure 8: Mean grass and shrub cover of the two vegetation clusters on the Observatory. All 20 plots were recorded each of the given years. Cluster 1: n=14 plots; Cluster 2: n=6 plots. Drawn in lines indicate temporal changes in cover, dotted lines represent the data gap for the years 2010-2012.

5.2. Comparison of study sites

5.2.1. Cover of grasses and thorn shrubs in 2013

Grass cover was very similar between the sites, even between bush cleared and untreated camps. Only on Kudu 2 grass cover was significantly higher than on the Observatory and Rehab East (Table 2). However, a high variability in grass cover was found within the single sites. On the Observatory grass cover ranged between 3 % and 50 %. Lowest grass cover on the cleared Rehab camp was 2.5 %, while highest was even 60 % (Figure 9, Table 2).

Thorn shrub cover was –not surprisingly- significantly higher on the uncleared test sites (Observatory and Rehab East) than on the cleared ones (Kudu 2 and Rehab; Table 2). No significant difference in thorn shrub cover was found between the two cleared or the two uncleared sites respectively. Thorn shrub cover was also highly variable within the uncleared sites, e.g. between 0 % and 47.5 % on Rehab East (Figure 9, Table 2).

Table 2: Results of Kruskal-Wallis and post-hoc tests (Mann-Whitney-U) for grass and thorn shrub cover values.

Grass cover		Kruskal-Wallis: $\chi^2=8.723$, $p=0.033$, $n=56$ plots		
Comparison	Mann-Whitney U	z	p	corrected p (Bonferroni-Holm)
Observatory - Kudu 2	41.5	-3.075	0.002	0.008
Kudu 2 - Rehab East	32.5	-2.294	0.022	0.010
Kudu 2 - Rehab	46.5	-1.480	0.139	0.013
Rehab - Rehab East	69.5	-1.440	0.885	0.017
Observatory - Rehab East	106.5	-0.527	0.598	0.025
Observatory - Rehab	111.5	-0.332	0.740	0.050

Thorn shrub cover		Kruskal-Wallis: $\chi^2=19.328$, $p<0.001$, $n=56$ plots		
Comparison	Mann-Whitney U	z	p	corrected p (Bonferroni-Holm)
Observatory - Rehab	31.5	-3.446	0.001	0.008
Observatory - Kudu 2	36.0	-3.270	0.001	0.010
Kudu 2 - Rehab East	27.5	-2.570	0.010	0.013
Rehab - Rehab East	29.0	-2.483	0.013	0.017
Kudu 2 - Rehab	52.0	-1.155	0.248	0.025
Observatory - Rehab East	96.0	-0.934	0.350	0.050

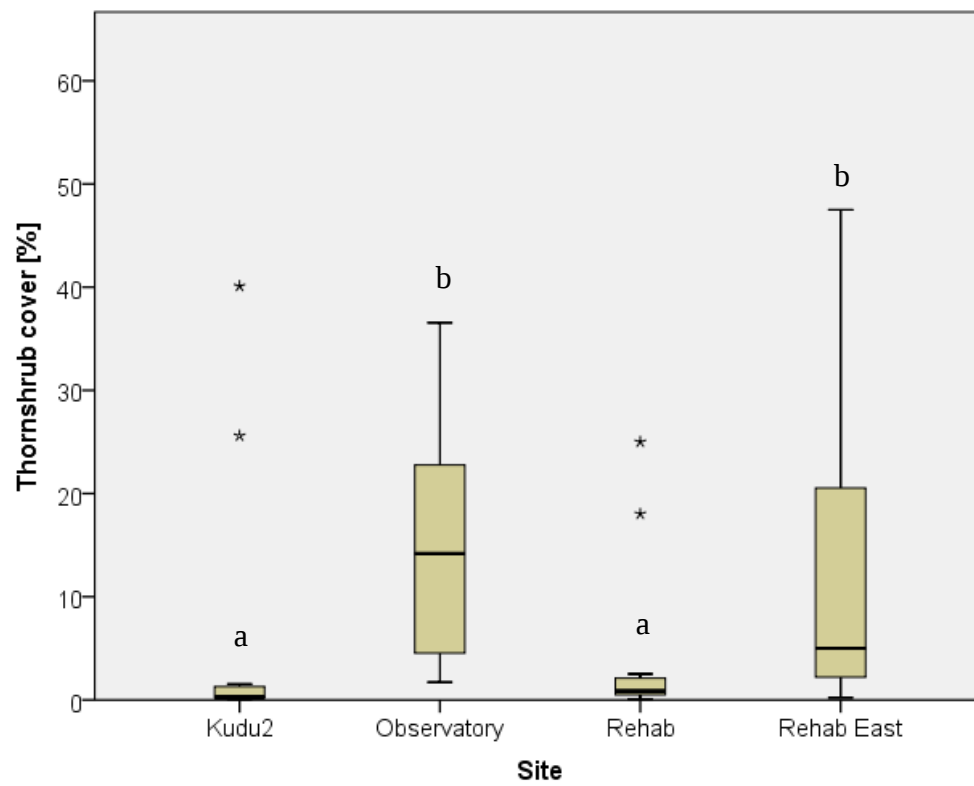
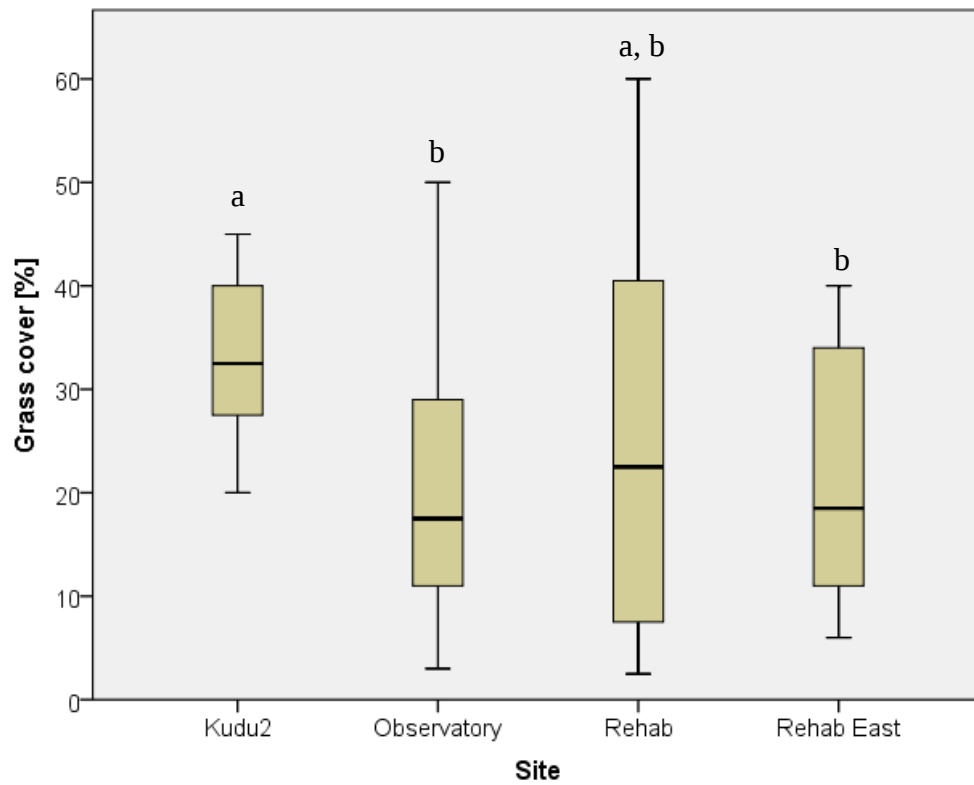


Figure 9: Grass cover and thorn shrub cover of the four test sites in 2013. Different small letters indicate significant differences at $p < 0.05$. Outliers in thorn shrub cover on Kudu 2 and Rehab are caused by large single trees. Observatory: $n=20$; Kudu 2, Rehab, and Rehab East: $n=12$.

5.2.2. Thorn shrub numbers per site in 2013

Acacia mellifera occurred on all sites in mentionable numbers. Mean counts ranged from 3 on Rehab to 10 on the Observatory. Even on the bush cleared Kudu 2, a mean of 6 individuals was counted per plot (Table 3). *A. hebeclada* numbers were generally much lower, only few individuals were found on the Observatory and Rehab East. *A. luederitzii/reficiens* was significantly more abundant on the Observatory than on all other sites. *A. tortilis* numbers were highest on Kudu 2, where large single trees were left out from clearing measures to serve as shade trees. *Dichrostachys cinerea* was found in small numbers on Rehab and Rehab East (Figure 10, Table 3, Table 4).

Highest thorn shrub numbers were found on the Observatory. *A. luederitzii/reficiens* was the most abundant thorn shrub there (mean count per plot: 14 individuals), followed by *A. mellifera*. Highest individual numbers on an Observatory plot were 195 Acacias, 169 of them juvenile individuals of *A. luederitzii/reficiens* (Figure 10, Table 3, Table 4).

Table 3: Mean thorn shrub counts per species and site in 2013, rounded to whole numbers. Observatory: n=20 plots; Kudu 2, Rehab, and Rehab East: n=12 plots.

Species	Observatory	Kudu 2	Rehab	Rehab East
<i>Acacia hebeclada</i>	1	0	0	0
<i>Acacia luederitzii/reficiens</i>	14	2	0	1
<i>Acacia mellifera</i>	10	6	3	4
<i>Acacia tortilis</i>	1	3	0	0
<i>Dichrostachys cinerea</i>	0	0	3	4

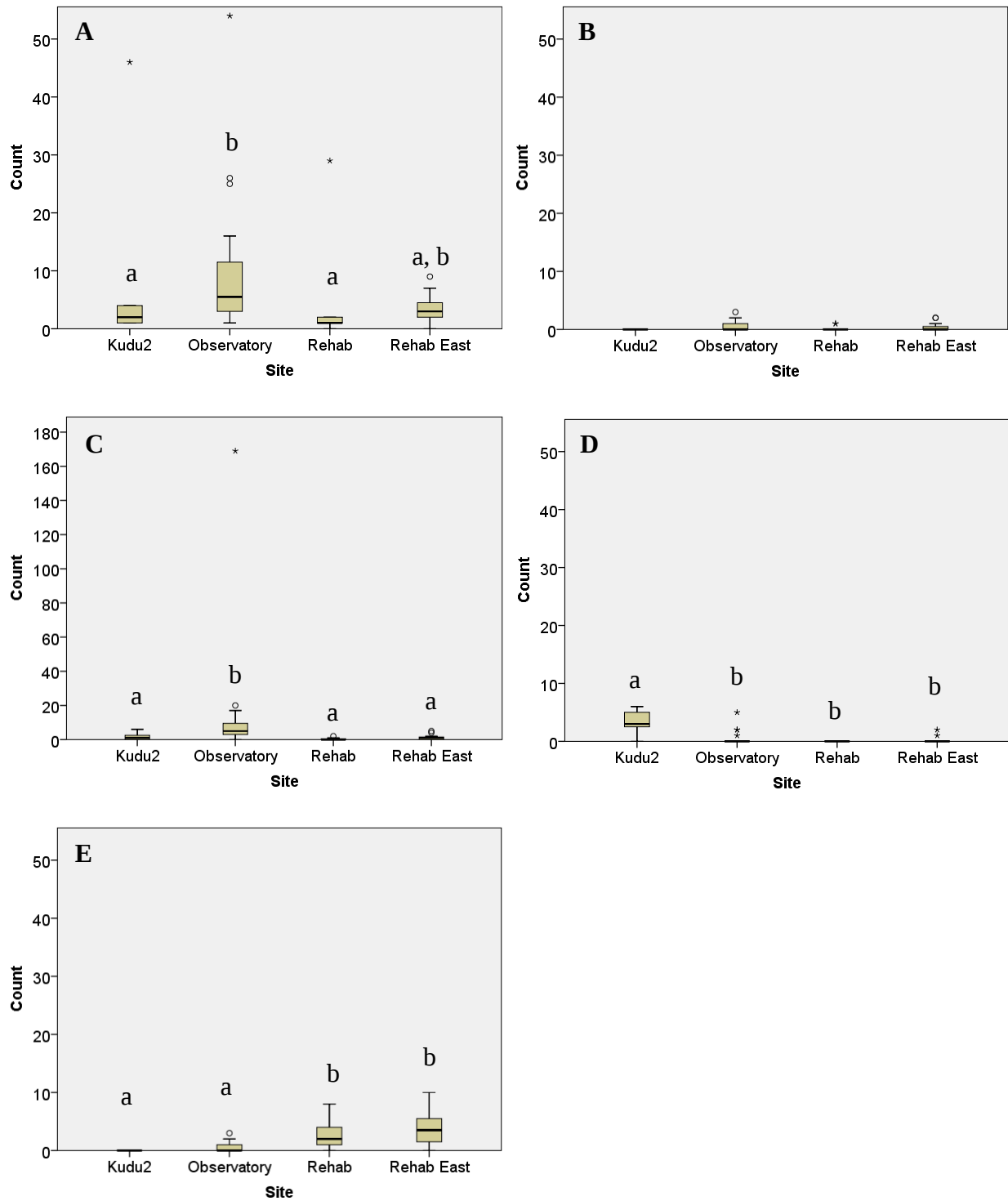


Figure 10: Individual numbers of thorn shrubs per site. Please note the different scaling for *Acacia luederitzii/reficiens*. A: *A. mellifera*; B: *A. hebeclada*; C: *A. luederitzii/reficiens*; D: *A. tortilis*; E: *D. cinerea*. Different small letters indicate significant differences at $p < 0.05$. Observatory: $n = 20$ plots; Kudu 2, Rehab, and Rehab East: $n = 12$ plots.

Table 4: Results of Kruskal-Wallis and post-hoc tests (Mann-Whitney U) for thorn shrub species distribution over sites in 2013.

<i>Acacia mellifera</i> Kruskal-Wallis: Chi ² =17.962, p<0.001, n=56 plots				
Comparison	Mann-Whitney U	z	p	corrected p (Bonferroni-Holm)
Observatory - Rehab	28.0	-3.609	<0.001	0.008
Observatory - Kudu 2	52.5	-2.645	0.008	0.010
Observatory - Rehab East	64.0	-2.192	0.028	0.013
Rehab - Rehab East	35.0	-2.169	0.030	0.017
Kudu 2 - Rehab	39.5	-1.966	0.049	0.025
Kudu 2 - Rehab East	58.5	-0.790	0.430	0.050
<i>Acacia hebeclada</i> Kruskal-Wallis: Chi ² =7.071, p=0.07, n=56 plots				
Comparison	Mann-Whitney U	z	p	corrected p (Bonferroni-Holm)
Observatory - Kudu 2	72.0	-2.465	0.014	0.008
Kudu 2 - Rehab East	54.0	-1.809	0.070	0.010
Observatory - Rehab	89.0	-1.480	0.139	0.013
Kudu - Rehab	60.0	-1.446	0.148	0.017
Observatory - Rehab East	104.5	-0.716	0.474	0.025
Rehab - Rehab East	64.0	-0.652	0.515	0.050
<i>Acacia luederitzii/reficiens</i> Kruskal-Wallis: Chi ² =25.383, p<0.001, n=56 plots				
Comparison	Mann-Whitney U	z	p	corrected p (Bonferroni-Holm)
Observatory - Rehab	12.0	-4.279	<0.001	0.008
Observatory - Rehab East	34.5	-3.358	0.001	0.010
Observatory - Kudu 2	44.5	-2.960	0.003	0.013
Rehab - Rehab East	40.5	-2.012	0.044	0.017
Kudu 2 - Rehab	42.5	-1.909	0.056	0.025
Kudu 2 - Rehab East	68.0	-0.241	0.810	0.050
<i>Acacia tortilis</i> Kruskal-Wallis: Chi ² =32.346, p<0.001, n=56 plots				
Comparison	Mann-Whitney U	z	p	corrected p (Bonferroni-Holm)
Observatory - Kudu 2	22.5	-4.129	<0.001	0.008
Kudu 2 - Rehab	6.0	-4.169	<0.001	0.010
Kudu 2 - Rehab East	8.0	-3.902	<0.001	0.013
Observatory - Rehab	96.0	-1.626	0.104	0.017
Rehab - Rehab East	60.0	-1.445	0.149	0.025
Observatory - Rehab East	114.5	-0.315	0.753	0.050

Table 4 (continued): Results of Kruskal-Wallis and post-hoc tests (Mann-Whitney U) for thorn shrub species distribution over sites in 2013.

<i>Dichrostachys cinerea</i>		Kruskal-Wallis: $\chi^2=31.276$, $p<0.001$, $n=56$ plots		
Comparison	Mann-Whitney U	z	p	corrected p (Bonferroni-Holm)
Observatory - Rehab East	23.5	-3.982	<0.001	0.008
Kudu 2 - Rehab	12.0	-3.879	<0.001	0.010
Kudu 2 - Rehab East	6.0	-4.157	<0.001	0.013
Observatory - Rehab	40.5	-3.327	0.001	0.017
Observatory - Kudu 2	84.0	-2.061	0.039	0.025
Rehab - Rehab East	52.5	-1.136	0.256	0.050

5.3. Habitat use of herbivores

5.3.1. Comparison of Rehab and Rehab East

The two sites Rehab and Rehab East are situated within the same camp next to each other and differ only in their management, i.e. bush clearing on Rehab and no such measures on Rehab East. Therefore pellet counts of these two related sites were compared to check for habitat preferences of herbivores, either for the open or the shrubbier habitat (Figure 11). Total counts (all species) did not differ between the sites (Mann-Whitney-U=53.0, $z=-1.10$, $p=0.271$, $n=24$ transects), nor was there a significant difference in pellet counts of warthog (Mann-Whitney-U= 58.5, $z=-0.785$, $p=0.432$, $n=24$ transects) or greater kudu (Mann-Whitney-U= 56.5, $z=-0.923$, $p=0.356$, $n=24$ transects). Oryx, however, differed significantly in distribution and preferred the cleared part of the camp (Mann-Whitney-U= 23.5, $z=-2.872$, $p=0.004$, $n=24$ transects).

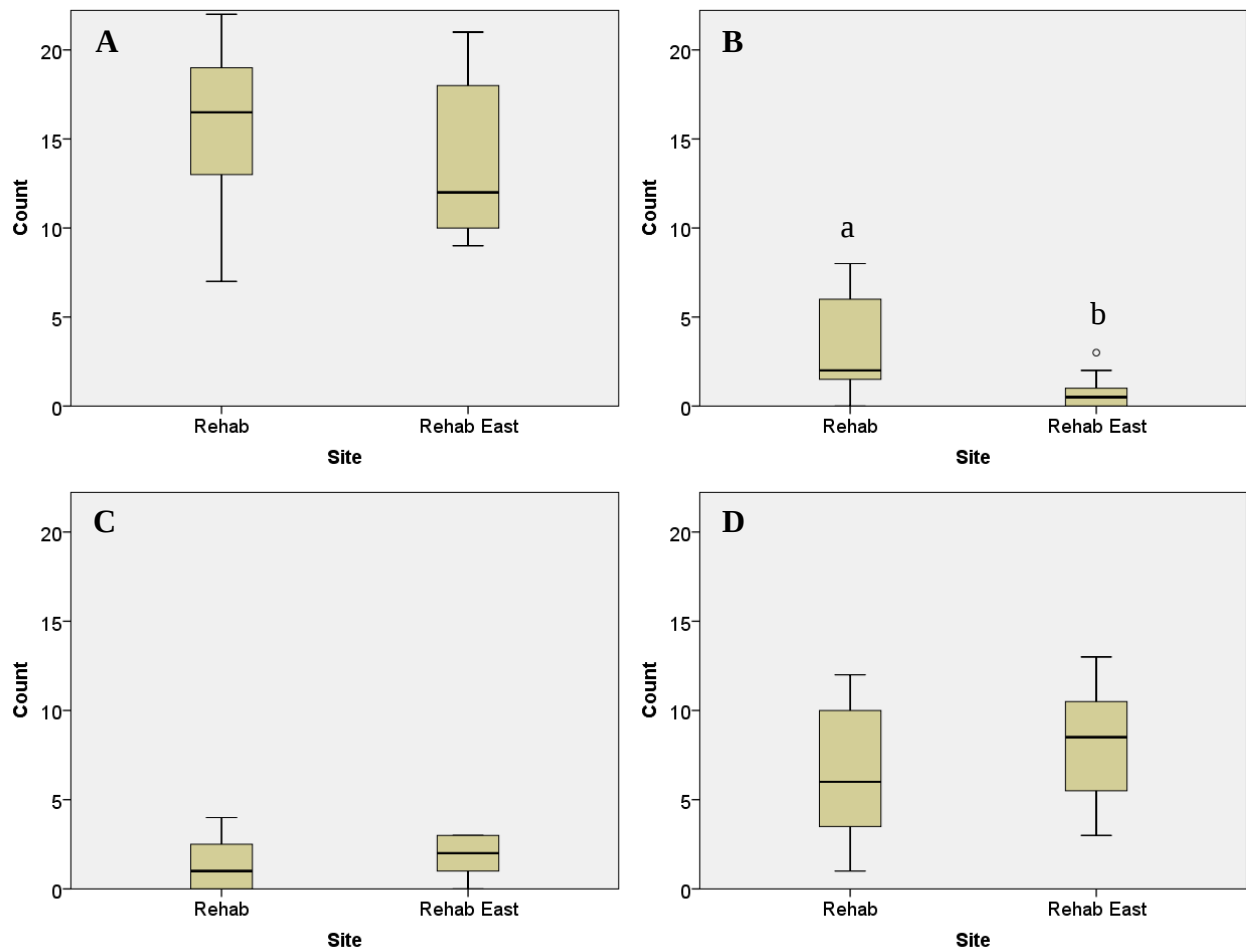


Figure 11: Fecal counts on Rehab and Rehab East. A: total count (all species, including unknown); B: Oryx; C: Kudu; D: Warthog. Different small letters indicate significant differences at $p < 0.05$. $n=12$ transects per site.

5.3.2. Species distribution over sites

The cleared site of Rehab camp was excluded from further analysis because of the spatial proximity of the two Rehab sites. Per species, a Kruskal-Wallis test was carried out, followed by multiple comparisons using a post-hoc test (Mann-Whitney U).

For oryx, counts were highest on the Observatory. The difference to Kudu 2 and Rehab East is significant at $p < 0.05$ (Figure 12, Table 5). The Observatory was also the only site where oryx dung middens were found. A total of 3 middens were counted there. Almost no oryx pellets were found on Kudu 2 and Rehab East.

Kudu pellet counts were found highest on Rehab East, followed by Kudu 2. Almost no kudu pellets were found on the Observatory. The difference between Rehab East and Observatory

is significant at $p < 0.05$ (Figure 12, Table 5). A slight opposing trend in the distribution of oryx and kudu is visible.

Warthog feces were found more frequent than those of the other species. Most warthog feces were found on the open camp Kudu 2, followed by the Observatory and Rehab East. Count between all three sites are significant different at $p < 0.05$ (Figure 12, Table 5).

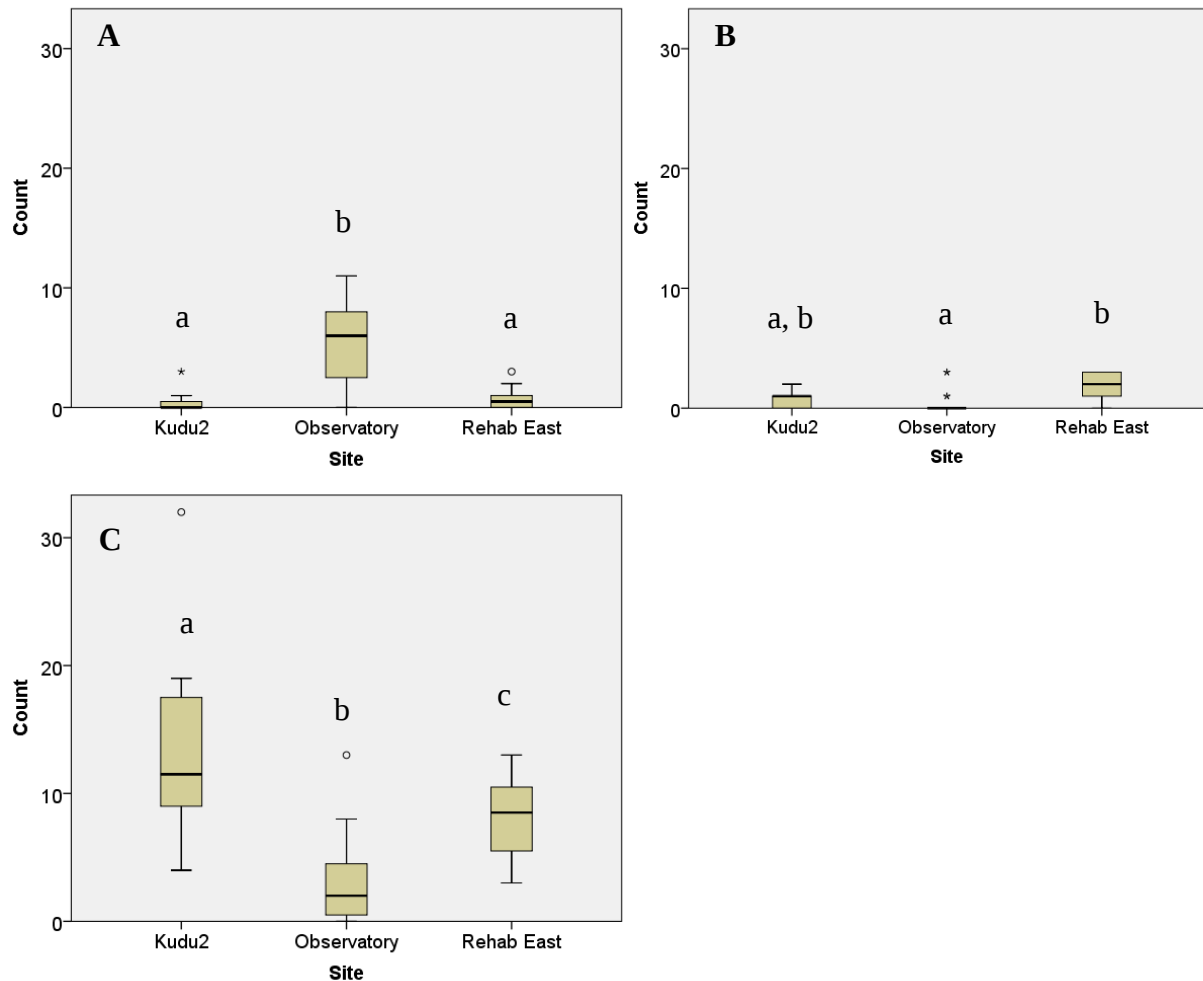


Figure 12: Pellet counts per study site. A: Oryx; B: Kudu; C: Warthog. Different small letters indicate significant differences at $p < 0.05$. Observatory: $n = 20$ transects; Kudu 2 and Rehab East: $n = 12$ transects.

Table 5: Results of Kruskal-Wallis and post-hoc tests (Mann-Whitney U) for herbivore distribution.

Monocotyledon particles		Kruskal-Wallis: $\chi^2=46.709$, $p<0.001$, $n=62$ fecal samples		
Comparison	Mann-Whitney U	z	P	corrected p (Bonferroni-Holm)
Kudu-Cattle	0.0	-4.887	<0.001	0.008
Kudu-Warthog	0.0	-4.887	<0.001	0.010
Oryx-Kudu	0.0	-4.823	<0.001	0.013
Oryx-Warthog	13.5	-4.211	<0.001	0.017
Oryx-Cattle	26.0	-3.716	<0.001	0.025
Cattle-Warthog	91.7	-1.376	0.169	0.050

Dicotyledon particles		Kruskal-Wallis: $\chi^2=55.424$, $p<0.001$, $n=62$ fecal samples		
Comparison	Mann-Whitney U	z	P	corrected p (Bonferroni-Holm)
Oryx-Warthog	0.0	-4.754	<0.001	0.008
Kudu-Warthog	0.0	-4.754	<0.001	0.010
Kudu-Cattle	0.0	-4.748	<0.001	0.013
Cattle-Warthog	4.5	-4.668	<0.001	0.017
Oryx-Cattle	5.0	-4.549	<0.001	0.025
Oryx-Kudu	10	-4.252	<0.001	0.050

5.3.3. Influence of thorn shrub cover, grass cover and sites on herbivore distribution

It was assumed that the distribution of herbivores is dependent on grass or thorn shrub cover respectively. Generalized Linear Models (GLMs) were carried out to test the influence of thorn shrub cover, grass cover and sites on animal distribution. For all species, corrected models were significant at $p<0.01$ or $p<0.001$, while thorn shrub cover and grass cover had no significant influence on herbivore distribution. For kudu, there was a slight trend for thorn shrub cover influencing animal distribution ($p=0.081$). For warthog, grass cover showed a similar trend ($p=0.100$; Table 6). Different sites showed a significant influence though (Table 6).

In addition to the GLMs, correlations between distribution of oryx and kudu were carried out. As the two species showed opposing trends in their distribution (Figure 12), it was tested if they influence or exclude each other to a certain degree. No such correlations could be found at a significant level (Spearman-Rho: $r_s^2 = -0.284$, $p=0.080$, $N=44$).

Table 6: GLMs for oryx, kudu and warthog.

Species: Oryx. a) R Squared=0.483 (Adjusted R Square =0.432)					
Source	Type III sum of squares	df	mean squares	F	p
Corrected model	275.007 ^a	5	55.001	9.359	0.000
Intercept	61.653	1	61.653	10.491	0.002
Grass cover	0.164	1	0.164	0.028	0.868
Thorn shrub cover	2.884	1	2.884	0.491	0.487
Site	233.490	3	77.830	13.244	0.000
Error	293.832	50	5.877		
Total	1055.000	56			
Corrected total	568.839	55			
Species: Kudu. b) R Squared=0.266 (Adjusted R Square =0.193)					
Source	Type III sum of squares	df	mean squares	F	p
Corrected model	19.691 ^b	5	3.938	3.630	0.007
Intercept	11.258	1	11.258	10.378	0.002
Grass cover	0.490	1	0.490	0.451	0.505
Thorn shrub cover	3.435	1	3.435	3.166	0.081
Site	18.120	3	6.040	5.568	0.002
Error	54.238	50	1.085		
Total	126.000	56			
Corrected total	73.929	55			
Species: Warthog. c) R Squared=0.485 (Adjusted R Square =0.434)					
Source	Type III sum of squares	df	mean squares	F	p
Corrected model	925.872 ^c	5	185.174	9.431	0.000
Intercept	305.187	1	305.187	15.544	0.000
Grass cover	55.252	1	55.252	2.814	0.100
Thorn shrub cover	17.235	1	17.235	0.878	0.353
Site	612.377	3	204.126	10.397	0.000
Error	981.682	50	19.634		
Total	4779.000	56			
Corrected total	1907.554	55			

5.4. Diet selection of herbivores

5.4.1. Plant fragments in feces and stomach content

The percentages of different plant fragments found in fecal samples are displayed in Figure 13. In cattle feces, 51 % grasses and 10.3 % dicot fragments were counted. Fragments of *Leucosphaera bainesii* (0.9 %) and other woody plants (0.2 %) were also found. In warthog feces, mostly grasses (69.4 %) but also a few dicot particles (1.6 %) were found. For oryx, the diet appears more mixed. The feces consisted of 19.0 % Poaceae fragments, 29.8 % dicots – including some woody fragments, and a notable portion of *Leucosphaera bainesii* (6.7 %). In kudu feces, 70.2 % of the particles were determined as dicot. Some woody fragments (3.2 %) and very few grasses (0.2 %) were also found. Between 26.3 % (kudu) and 43.8 % (oryx) of the particles remained undetermined.

The numbers of monocot and dicot fragments found in feces are summarized in Figure 15. Cattle and warthog do not significantly differ in the proportion of monocot particles. Oryx can be distinguished with $p < 0.05$ from all other species (Figure 15, Table 7).

For dicot fragments, all species differ significantly. Highest proportion was found in kudu feces, followed by oryx (Figure 15, Table 7). Cattle and warthog feces contained only few dicot particles.

In stomach content samples, percentages of Poaceae fragments were found much higher than in the feces (Figure 14). This difference is widest for oryx: Almost all fragments in rumen content were identified as Poaceae (96.8 %), whereas the feces data show rather a mixed diet pattern.

For cattle rumen content, 78.6 % Poaceae, 5.9 % dicot and 3.6 % woody particles were identified. In warthog stomach content, 88.6 % Poaceae fragments were counted, with a few woody (0.8 %) and other dicot (3.8 %) particles. Due to the larger particle size, the proportion of undetermined particles ranges between only 2.3 % (oryx) and 12 % (cattle).

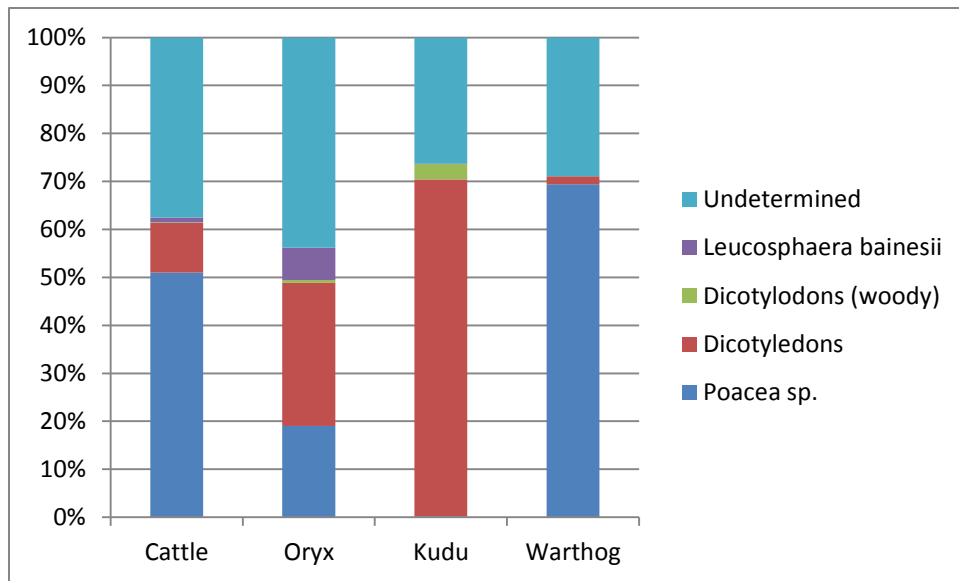


Figure 13: Mean numbers of plant fragments found in herbivore feces. Cattle and warthog: n=16; Oryx and kudu: n=15.

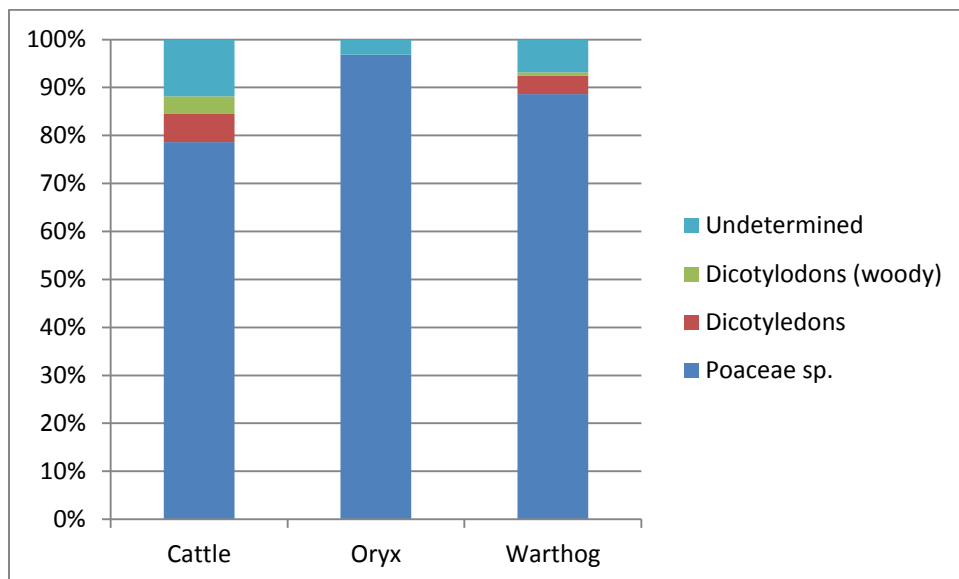


Figure 14: Mean numbers of plant fragments found in herbivore stomach/rumen content. Cattle and warthog: n=1; Oryx: n=7.

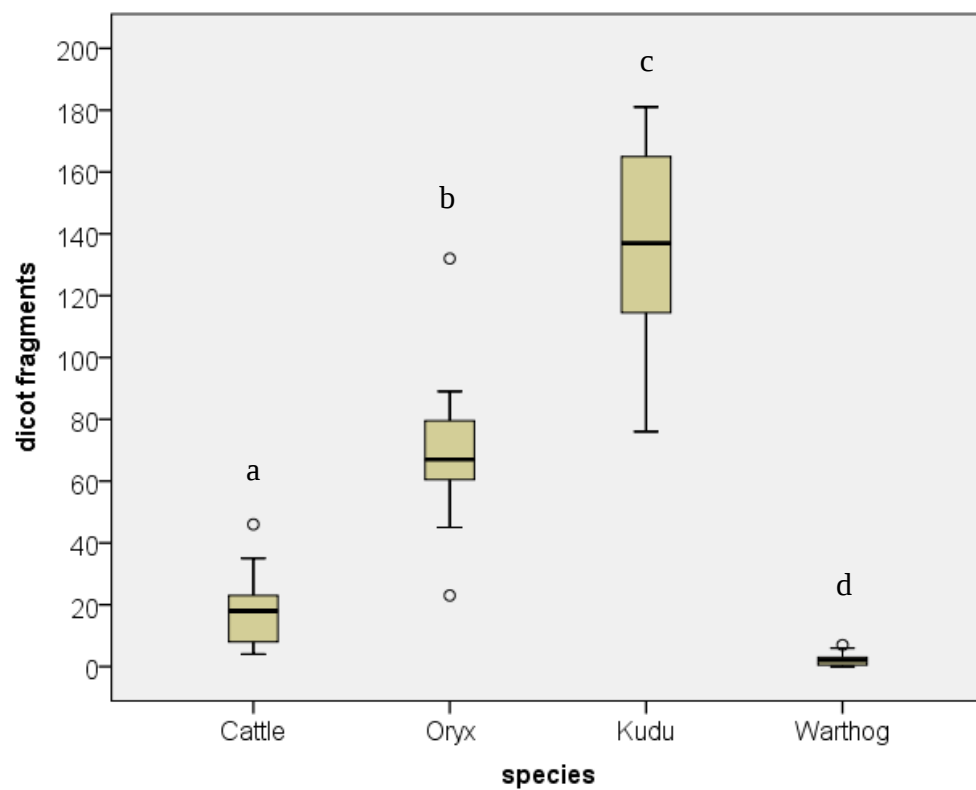
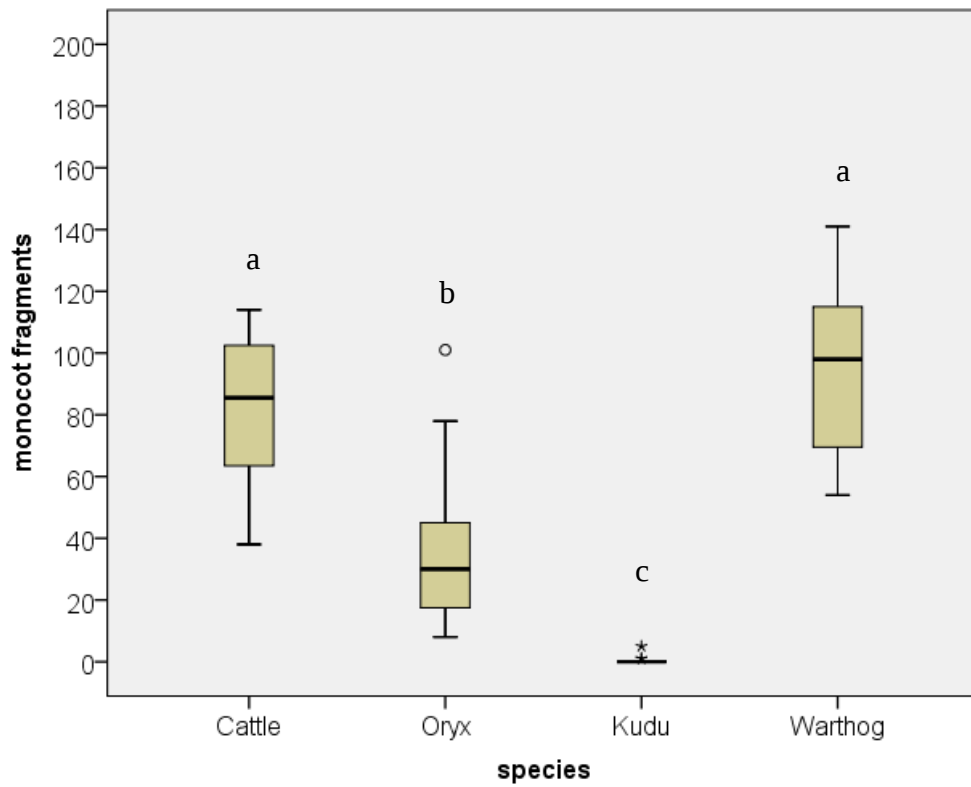


Figure 15: Number of monocot and dicot fragments found in herbivore feces. Different small letters indicate significant differences at $p < 0.05$. Cattle and warthog: $n=16$; Oryx and kudu: $n=15$.

Table 7: Results of Kruskal-Wallis and post-hoc tests (Mann-Whitney U) for monocot and dicot particles in feces. Warthog and cattle: n=16; Kudu and oryx: n=15.

Monocotyledon particles		Kruskal-Wallis: $\chi^2=46.709$, $p<0.001$, n=62 fecal samples		
Comparison	Mann-Whitney U	z	p	corrected p (Bonferroni-Holm)
Kudu-Cattle	0.0	-4.887	<0.001	0.008
Kudu-Warthog	0.0	-4.887	<0.001	0.010
Oryx-Kudu	0.0	-4.823	<0.001	0.013
Oryx-Warthog	13.5	-4.211	<0.001	0.017
Oryx-Cattle	26.0	-3.716	<0.001	0.025
Cattle-Warthog	91.7	-1.376	0.169	0.050

Dicotyledon particles		Kruskal-Wallis: $\chi^2=55.424$, $p<0.001$, n=62 fecal samples		
Comparison	Mann-Whitney U	z	p	corrected p (Bonferroni-Holm)
Oryx-Warthog	0.0	-4.754	<0.001	0.008
Kudu-Warthog	0.0	-4.754	<0.001	0.010
Kudu-Cattle	0.0	-4.748	<0.001	0.013
Cattle-Warthog	4.5	-4.668	<0.001	0.017
Oryx-Cattle	5.0	-4.549	<0.001	0.025
Oryx-Kudu	10	-4.252	<0.001	0.050

5.4.2. List of plant species

It was generally not possible to determine the plant fragments quantitatively to a species or even genera level, neither in the feces nor in the stomach content. However, in a few cases identification was possible, although the number of fragments was too small for further analysis. The determined species are listed in Table 8 and can give an idea of the eaten species.

Table 8: Species found in herbivore feces and stomach content. (+): species was found in feces and/or stomach content.

	Species	Cattle	Oryx	Kudu	Warthog
Monocot	<i>Aristida cf. congesta</i>		+		+
	<i>Aristida congesta</i>	+			
	<i>Aristida sp.</i>	+			+
	<i>Eragrostis sp.</i>		+		+
	<i>Melinis repens</i>	+			
	<i>Stipagrostis cf. uniplumis</i>	+			
	<i>Stipagrostis sp.</i>	+			+
Dicot	cf. <i>Acacia sp.</i>	+		+	
	<i>Boscia albitrunca</i>		+		
	<i>Grewia flava</i>		+	+	
	Lamiaceae sp.	+			
	<i>Leucosphaera bainesii</i>	+	+		

6. DISCUSSION

6.1. How did the observatory develop over the last decade?

It was analyzed if there was a change in thorn shrub cover or grass cover on the Observatory plots during the last decade. None of the single thorn shrub species (*Acacia* spp., *Dichrostachys cinerea*) increased in cover and also the total cover of all thorn shrubs was constant over time. Grass cover on the other hand was highly variable and fluctuated with rainfall.

Cluster analysis showed that both patches with low thorn shrub cover and with high thorn shrub cover occur on the Observatory. The comparison of these clusters with the major soil types on the Observatory (from Jürgens et al. 2010) remained inconclusive. This excludes soil moisture and nutrient availability as drivers, since these factors are closely related to soil types. Microclimate can also be rejected as a possible explanation, as the Observatory covers a relatively small plain. There are no differences in management on the Observatory, and fires did not occur in the area during the previous years. However, it must be noted that the monitoring period of about a decade is relatively short compared with the time needed for establishment of trees, and might have not been long enough to observe significant changes in cover of woody plants.

Still, at Olifants Drift in Botswana, where vegetation composition is similar to Erichsfelde, bush encroachment could be observed after a period of 12-13 years (van Vegten 1983). Over 25 years, woody biomass had almost tripled (van Vegten 1983). Knoop & Walker (1985) estimated a period of 5-10 years for *Acacia* seedlings to grow a closed canopy. The herbaceous layer at Olifants Drift was cleared though, so seedlings had little competition from the grass layer. Anyhow, changes in shrub cover should be visible within a decade.

On the shrubby plots (cluster 2), woody cover averaged about 30 %, which corresponds exactly to the maximum equilibrium woody cover of semi-arid savannas reported by Meyer et al. (2007, cited in Russel & Ward 2014). Russel & Ward (2014), according to this reference value, rated an area as encroached when woody cover exceeded 40 %. This suggests the Observatory to be still in a state of equilibrium between grasses and trees.

According to the two-layer model of root niche-separation (Walter 1954, Walter & Volk 1954), shrub cover should increase directly when grasses are reduced by grazing or drought as happened in 2006. This could not be observed though. An alternative equilibrium theory is the balanced competition concept, which assumes the intraspecific competition for resources to

be more important than niche separation between grasses and woody plants (Scholes & Archer 1997, House et al. 2003). As stated in this model, tree density will increase until it is limited by competition with other trees, but still allows coexistence with other life forms (Scholes & Archer 1997). The situation on the shrubby patches could thus be regarded as a balanced equilibrium. However, this does not fully explain the occurrence of plots with low shrub cover.

State-and-transition models regard savannas as patchy systems that are stable on the landscape-scale and in which different transition states between grasslands and woody dominance occur (Scholes & Archer 1997, Wiegand et al. 2005, Britz & Ward 2007, Dougill et al. 1999). Disturbances and changes in environmental condition trigger the change from one equilibrium point to the other (House et al. 2003, Walker & Noy-Meir 1982). Accordingly, the situation on the Observatory can be regarded as mosaic of patches in different states, explaining the coexistence of both open and dense patches despite of similar environmental conditions like rainfall and grazing regime.

Joubert et al. (2008) pointed out that transitions between states are closely related to recruitment events, which require certain environmental conditions. Patches with higher densities of thorn shrubs could then be explained by small-scale differences in recruitment, e.g. the presence or absence of parent trees. For *A. mellifera*, one of the most abundant (and problematic) thorn shrubs on Erichsfelde, recruitment requires three consecutive years of good rainfall (Joubert et al. 2008). The first year is needed for sufficient production of viable seeds, because only after high rainfall events seed banks are large enough to endure predation (Joubert et al. 2008). In the second year seedlings germinate and establish, while the third year of above-average rainfall secures the survival of a high proportion of seedlings (Joubert et al. 2008). Such events are rare, and the landscape will thus consist of patches in different states, depending on the success or failure of transition on a particular patch (Joubert et al. 2008).

In addition, the coexistence of grasses and trees in savannas is often attributed to the mean annual precipitation (MAP; Walter 1954, Sankaran et al. 2005, Rohde & Hoffman 2012, Ward et al. 2013). Sankaran et al. (2005) regarded savannas with a MAP below 650 mm as “climatically determined” and thus stable, meaning that no external impacts like fire or herbivory are needed to preserve the coexistence between grasses and shrubs. Fire, herbivory, and soil properties in such stable savannas are thus only additional factors, which can keep woody vegetation below the theoretically possible amount (Sankaran et al. 2005). This could also explain why no further encroachment could be observed on Erichsfelde, were the MAP is

about 350 mm. Rohde & Hoffman (2012), however, gave a threshold of around 250 mm MAP for stable vegetation, and ascribe increases in tree cover above this threshold to the rainfall gradient, land-use regimes and the increase in atmospheric CO₂. The effect of slowly increasing atmospheric CO₂-fertilization would nevertheless only be visible over a larger time span and cannot be assessed within a decade.

The high variability of grass cover with rainfall can be explained by the life cycle of grasses. Due to their extensive root system, they can only uptake water and thus start growing when the soil is sufficiently wet (Walter 1954). In times of drought, grass growth is limited by water availability in the topsoil and thus related to the amount of rainfall. On the Observatory, recovering of grasses after the sparse rainy season 2006/2007 took at least 3 years (2007-2009). It is likely that grasses became over-utilized in the year of drought, and germination from seedbanks or resprouting from remaining tussocks needed more than one year. A reduced grass layer can also be the trigger for increased tree recruitment (Walter 1954, Scholes & Archer 1997). However, no increase in thorn shrub cover could be observed. The overall appearance of results indicates that the current management practices on the farm support a stable state and prevent additional encroachment.

It should be noted that different months of observation may have altered the cover estimates of grasses to a certain extent, as the time of data collection varied between years from April to June. This is discussed in chapter 6.5.1.

6.2. How do grass cover and thorn shrub densities differ between the study sites?

The four study sites on Erichsfelde were compared in terms of thorn shrub densities and grass cover. Thorn shrub cover values were naturally lower on the bush cleared sites; therefore sites were compared in terms of individual numbers.

Highest densities of thorn shrubs were found on the Observatory, with *Acacia mellifera* and *Acacia luederitzii/reficiens* as most abundant species. For the latter, highest count were 169 individuals on 100m², most of them juvenile individuals and saplings. Both species are reported to have shallow lateral roots, leading to a better access to nutrients and water also from the upper soil layers (Skarpe 1990a) and giving them a competitive advance.

The high numbers of small, juvenile *A. mellifera* and *A. luederitzii/reficiens* imply a potential for future encroachment. Seedlings and saplings are in direct competition with grasses, thus escaping the herbaceous layer is a critical state in tree recruitment (Scholes & Archer 1997)

and saplings can be trapped there for years by herbivory or fires (Bond 2008). If the grass layer is reduced by overgrazing or drought, saplings might quickly develop to bushes and trees (Scholes & Archer 1997, O'Connor et al. 2014). A dense grass layer can also provide fuel for fires that prevent saplings from growing above the herbaceous layer (Scholes & Archer 1997, Joubert et al. 2008, Higgins et al. 2000). Fires, however, did not occur on the study sites in the previous years.

On both cleared sites (Kudu 2 and Rehab), where clearing was done two and a half years before the study, thorn shrub densities were about as high as on the uncleared Rehab East. As, in contrast to the Observatory, there is little competition with adult trees, adjusted management might be necessary to prevent future growth of shrubs and trees on these camps. Due to seeding of grasses on the bush cleared sites, grass cover was expected to be higher than on the untreated sites. However, this effect was only weak: two and a half years after clearing and seeding grass cover on the cleared sites was only slightly higher. Results were significant for Kudu 2, but not for Rehab. However, seeding on Rehab was not too successful due to poor rainfall after seeding (farm manager Rudi Scheidt, pers. comm.). It must also be considered that the study year (2013) was outstandingly dry and conditions differ in years with higher rain fall.

In addition, it is often discussed that trees and shrubs can serve as a shelter for perennial grasses. Scholes and Archer (1997) listed both examples for grass growth reduced by trees or increased by trees. They suggested that thorny shrubs may protect palatable grasses from grazing herbivores. Herbs and grasses in open areas are more easily accessible than those growing beneath shrubs (Jaksić & Fuentes 1980). In the present study, tufts of grasses could often be observed growing within *Acacia* or *Dichrostachys* shrubs, but this was not systematically assessed. Weltzin & Coughenour (1990) in Kenya found herbaceous biomass higher under tree canopies than in the inter-tree areas. They ascribed this phenomenon to shading, lower soil temperature, lower water stress, and higher nutrient concentrations near the stem. Stemflow of rainwater, from the canopy to the base, can also increase water availability under trees (Walker et al. 1981). Thus, the effect of woody plants on grass growth is not always suppressive, but can also be neutral or positive (Scholes & Archer 1997).

6.3. Do herbivore species have a preference for open or shrubby habitats?

The distribution of warthog, oryx, and greater kudu during the dry season was estimated using pellet counts. It was assumed that grazers would prefer open, grassy habitats while browsers should favor shrubbier areas. Accordingly, warthog and oryx should have favored open grassy areas, and kudu should have been associated with denser savanna vegetation. Such habitat preferences are already well described for the study species (Hofmann 1973, Bothma et al. 2010). However, no connection could be deduced between herbivore distribution patterns and grass or thorn shrub cover in this study. Although kudu and warthog, as expected, preferred a shrubby and an open site respectively (kudu: Rehab East, warthog: Kudu 2), oryx favored the rather shrubby Observatory. Results of the GLM showed that the site was a much more important factor for herbivore distribution than the amount of grasses or thorn shrubs. Still, for kudu and warthog there was a slight trend for grass and shrub cover to explain their distribution. Other studies found clearer distributional patterns, and identified drivers such as inter- and intraspecific competition or habitat type (e.g. Ben-Shahar 1992, Dörgeleh 2001). Dekker et al. (1996) studied herbivore distribution throughout different plant communities in the Mopani veld and found a clear spatial separation in the habitat use of several ungulate species, which became even distinct in the dry season, when resources are limited.

Animal behavior, however, is not only influenced by vegetation and forage availability, but also a vast number of other factors, such as water availability, shade, and presence of carnivores that have not been considered here (Pienaar 1974, Bergström & Skarpe 1999). Ford et al. (2014) described in detail the interaction between large carnivores, their herbivore prey and tree communities. Their study discovered risk avoidance (i.e. avoidance of carnivores) as driver of impala habitat selection. Absence of impala subsequently increased the prevalence of poorly defended trees, meaning their numbers increased in relation to well-defended more thorny species. Especially for oryx, which are regularly hunted on Erichsfelde and preferred the rather shrubby Observatory, risk avoidance could be a factor in habitat selection and drive them to prefer thickets over open areas.

In addition, habitat preferences strongly depend on structural diversity and spatial scales (Skarpe 1991) that were not assessed in this study. The correlation of herbivore distribution with site, but not with vegetation, suggests scale dependent features as driver of habitat use. Greenacre & Vrba (1984) pointed out that the “large-scale physiognomy” of a landscape is much more important for habitat frequentation than particular, small-scale patches of

vegetation. However, due to the high number of transects used per study site, assessment was rather comprehensive. It is possible, though, that the size of the studied camps or even the farm was still too small to cover the decision scale of the studied species. For Rehab and Rehab East, the spatial proximity of the two sites might also be a source of bias.

Further, animals do not necessarily drop their pellets where they feed. This applies mainly to species that utilize dung middens. Except for middens of male territorial oryx (Stuart & Stuart 2013), however, this does not apply to the species studied here.

6.4. What are the preferred feeding sources of game and cattle in the study area during the dry season?

It was aimed to determine the diet composition of cattle, oryx, greater kudu, and warthog to explore the impact of these species on bush encroachment and to determine the consumption of thorn shrub species by different herbivores. Only in a few cases it was possible to determine plant fragments in the samples to species level. Discrepancies occurred between data obtained from feces and from stomach content, with the proportion of monocotyledons generally found higher in stomach content. Possible reasons for this are discussed in chapter 6.5.2.

Cattle are grass and roughage eaters, and consume forage high in fiber (Hofmann 1989). Monocot fraction in the present study averaged 50 % in feces and almost 80 % in rumen content. Dicot fraction was about 10 % each. This is a much lower share as in literature, where proportions of 70 % monocot and 30% dicot are given for the dry season (Owen-Smith 1999). During the dry season, when availability of grasses is low, cattle have been observed to spend as much as 50-80 % of their feeding time browsing (Katjiua & Ward 2006). Moleele et al. (1998) found the time cattle spent browsing and litter foraging during the dry season equivalent to the time spent grazing. Preferred browse species in their study were *Dichrostachys cinerea* and *Grewia flava*, that both are present on Erichsfelde. It is possible that part of the deviation between the present and other studies arises from the undetermined fraction in feces, as dicot fragments are often underestimated (Henley et al. 2001). However, the high proportion of grasses found in cattle diet even during the dry season might also indicate a good availability of perennial grasses in the area.

Oryx is mainly referred to as bulk and roughage grazer (Hofmann 1989, Bothma et al. 2010) and thus seen as competitor for cattle. Hofmann & Stewart (1972) found almost entirely grasses in their diet, and Hofmann (1973) considered it “unlikely that oryx eat much browse”.

Nevertheless, they are frequently reported to feed also on browse, bulbs, tubers, rhizomes, and fruits, especially during the dry season (Hofmann 1973 and citations therein, Bothma et al. 2010). Owen-Smith (1999) indicated a diet composition of 78 % monocot and 22 % dicot material during the dry season. Browsed species include amongst other *Boscia albitrunca*, *Acacia* spp., and *Ehretia rigida* (Hofmann 1973). Gagnon & Chew (2000) expanded the concept of Hofmann and classified oryx as “variable grazer”, showing a high seasonal and geographical variability in their food spectrum, with the monocot share ranging between 60 and 90 %.

In oryx samples, the biggest discrepancy between feces and rumen occurred. Results from rumen analysis suggest a diet that entirely consisted of grasses. From fecal analysis, however, the diet appears more mixed and the amount of monocots in oryx diet was found to be much lower than in the literature, with 20 % monocot fragments and 35 % dicot fragments counted. It is assumed that for oryx the results of the fecal samples are more trustworthy, as dicot fragments could be identified rather clearly. In addition, although no dicot particles were recorded in the rumen samples, some were observed in several oryx rumens during sampling. As already mentioned for cattle, it must be noted that dicot fragments often are underestimated in fecal analysis, as they are normally more easily digestible than fiber-rich grasses (Lewis 1994, Henley et al. 2001). Such systematical bias can be excluded here though, as the share of dicot fragments in feces, compared with literature values, was higher in oryx feces, but was lower for cattle.

Leucosphaera bainesii was frequently recorded in the dicot fraction of oryx feces. This plant is of high nutritive value even during the dry season, containing about 3% digestible protein even when dry and up to 10 % when fresh (Walter & Volk 1954). The high proportion of dicot forage found in oryx feces may indicate that the “variable grazer” concept of Gagnon and Chew (2000) is more plausible than Hofmann’s classification as bulk and roughage grazer (see also Bodmer 1990). The food competition with cattle might thus be lower than generally assumed, but depends also on individual numbers that have not been assessed here.

Greater kudu are reported to feed on a huge spectrum of browse, but also fruits and forbs. Foraged species include amongst others *Acacia* spp., *Dichrostachys cinerea*, and *Combretum* spp. (Hofmann 1973, Bothma et al. 2010). A share of 85-90 % browse is given in the literature (Owen-Smith 1999, Gagnon & Chew 2000). They were classified as concentrate selector by Hofmann (1989), while Gagnon & Chew (2000) consider them as mixed-feeder generalists, consuming >20% of each monocots, dicots and fruits when available. During the

dry season, however, forage availability is restricted. Virtually no grasses were found in kudu feces, the identified particles consisted almost exclusively of browse.

Warthog are described as omnivorous mixed feeders (Bothma et al. 2010). In this study, their diet consisted almost exclusively of grasses, only very few dicot fragments were found. Results were similar between samples of feces and stomach content. Dicot particles were rarely and animal material was not found. Only little literature is available on the exact composition of their diet (e.g. Treydte et al. 2006). Depending on individual numbers, food competition with cattle for grasses might occur.

6.5. Methodological critique

6.5.1. Botanical methods

The dynamics of savanna systems are highly dependent on the spatial but also on the temporal scale, and long-term changes like bush encroachment can only be studied over time. Small-scale observations might miss evidence for landscape stability that becomes clearer on a larger scale (Skarpe 1992, Scholes & Archer 1997, Dougill et al. 1999, House et al. 2003). This highlights the need for longtime monitoring, including data on vegetation, soil properties, weather and pastoral production figures (Dougill et al. 1999). However, longtime observations like on the former BIOTA observatories involve a certain bias. Species determination can vary between observers, amongst others depending on their experience. This happened on the Erichsfelde observatory in the case of *Acacia reficiens* and *Acacia luederitzii* (see chapter 4.2). Also estimations of cover can be variable. Cover estimates are one of the standard methods in botany as they are uncomplicated and inexpensive. Nonetheless, estimates are no exact measure and thus involve bias. Cover estimates vary between observers and even between relevés made by a single person or team (e.g. Kercher et al. 2003). Another challenge is the yearly recording that –due to organizational constraints– cannot always be carried out at exactly the same time of the year. In the case of this study, the data recording period ranged from April to June. This can bias the results when for example cover values of grasses are compared, as cover values may vary between early (April) and mid dry season (June) due to water availability and grazing. In addition, financial constraints can lead to data gaps when the observatory cannot be recorded every year or at least in sufficient periods.

However, longtime monitoring observatories are a valuable source of time dependent data. To maintain the quality of data obtained, intensive training of observers, and long-term planning in terms of staff and financing could overcome these challenges.

6.5.2. Zoological methods

In the present study, diet composition was estimated by microscopic analysis of stomach content and feces. Stomach content was counted out without further treatment, while fecal samples were ground and then bleached using a solution of chloral hydrate prior to microscopic determination (see chapter 4.6 and 4.7).

This method was successfully applied in other ecosystems and for other ruminants (Juwig 2015, Porsiel 2015). However, results in the present study were not as detailed as expected. Determination of particles was widely restricted to the monocot/dicot level. In addition, a huge incongruity was found between the data derived from feces and stomach content analysis, e.g. 19% versus 96% Poaceae fraction in oryx feces and rumen respectively (see chapter 5.4). A reasonable amount of particles in the feces remained unidentified. It is thinkable that this fraction included mainly Poaceae fragments and consequently explains part of the differences between the two analyses. Such systematical bias can be excluded here though, as the share of dicot fragments in feces, compared with literature values, was higher in oryx feces, but was lower for cattle. In addition, Poaceae fragments are rather easy to recognize, and it is more likely to underestimate dicot material in fecal analysis (Henley et al. 2001).

For warthog and cattle data the small sample size of stomach samples ($n=1$) must also be considered. However, sample size of oryx rumen was $n=7$, which is reasonably representative. Stomach content and feces were analyzed using different methods and different microscopes in terms of magnification (stereo versus transmitted light microscope), which may have led to deviating results. Particle size in stomach content is considerably larger and more variable than in feces. Fecal samples in contrast were ground, resulting in smaller and more homogenously sized particles. The highly varying size of fragments could be a source of bias at this point, as particle size was not measured.

Particles in stomach content and feces are in different states of digestion, and different food components are digested to a varying extent (Stewart 1967, Henley et al. 2001). In addition, the time of gut transition can vary between forage species (Henley et al. 2001). Depending on their digestibility, pieces of plant material will decay to higher or lower amounts of particles,

altering their frequency in feces (Henley et al. 2001). Dicot fragments are thus often underestimated in fecal analysis (Lewis 1994, Henley et al. 2001), as they normally are more easily digestible than fiber-rich grasses. During the dry season, however, dicot browse mainly consists of lignified particles that often cannot be determined. Staining of the samples could then facilitate analysis.

Furthermore, determination of epidermal fragments requires sufficiently large particles in both references and samples that contain enough epidermal characteristics of that particular species. Only few such large fragments were found in the samples, compared with the total number of fragments counted. Most particles were rather small and did not show all characteristics needed for determination. Grinding of reference samples with a ball mill produced rather fine particles not always suitable for reference purpose. Fine sieving of samples and discarding of the fine fraction could overcome this. This was appropriate in the above mentioned studies of Juwig (2015) and Porsiel (2015), where an impact mill with an integrated sieve was used.

Another source of error might be the sampling of rumen content. In oryx rumen samples, no dicot fragments were found although some dicot leaves could be observed in the rumen during samples. As only small portions of the total volume were used for analysis, stratification of stomach content may have adulterated the results. Using mixed samples derived from different strata of the rumen might have avoided this problem. Stomach content also contains mainly plants that were consumed during the last few feeding periods before collection, whereas in fecal samples forage of a longer period is concentrated (Anthony & Smith 1974). Thus, deviation in the species composition or frequency of particles can occur.

As determination of particles was very difficult in feces, single plant hairs were counted to extend the range of evaluable fragments. As hairs can occur in very high numbers on plant surfaces, this also might have biased the result.

However, a huge number of studies from different ecosystems exist, which successfully determined diet composition to species level from epidermal characteristics (e.g. Stewart 1967, Kok & van der Schijff 1973, Barthlott & Martens 1979, Ellis 1979, Lensing 1979, Lensing 1982, García-González 1984, Treydte et al. 2006). Many of these studies focused on grazing animals and therefore have been limited to the characteristics of grasses. Stewart (1967), although successful in his determinations, described the problem of determination from other studies and pointed out that the microhistological method is usually applied in ecosystems of lower plant and animal diversity. In this context, it is also likely that the number of reference species has been too low in the present study.

The histological identification of plant fragments from feces requires a long training period and time-consuming preparation of reference material and samples in order to display epidermal features. Other methods for the determination of diet composition from feces include genetic analysis and the chemical analysis of n-alkanes (Dove & Mayes 1996, 2006). These substances occur in specific patterns in the cuticular waxes of plants and remain virtually undigested by herbivores. Thus, diet composition can be estimated by comparison of n-alkane patterns between plants and feces, but only if the number of possible food plants is low (Dove & Mayes 1996, 2006, Schwarz 2011). Both genetic analysis and analysis of n-alkanes are cost-intensive due to the chemicals needed and give only qualitative data. Thus, microscopic analysis is still a valuable method, as it is inexpensive and allows a semi-quantitative assessment of samples.

6.6. Outlook

Currently, the Observatory seems to be in equilibrium of grasses and trees and no further encroachment could be observed over the last decade. However, high densities of *Acacia mellifera* and *A. luederitzii/reficiens* saplings on single patches imply the possibility of future encroachment. Further monitoring, e.g. of single individuals, could help to assess recruitment dynamics.

In addition, further knowledge on herbivore food preferences would be advantageous. It was originally aimed to analyze which herbivore species feed on potential encroaching plants, as under certain condition browsing species can control the growth of shrubs and trees (Bester & Reed 1997, Jeltsch et al. 2000, Staver et al. 2009). This was not successful though due to methodological constraints. Further research on this topic should thus consider possible deviations between stomach content and fecal samples and evaluate the applicability of further methods. Comparison of food preferences with stocking numbers and game counts could give information about the actual food competition between cattle, oryx and warthog, depending on individual numbers. All three species feed mainly on grass, although in the present study oryx showed a more variable diet composition than the other two species. In this context, monitoring of diet compositions during different seasons would also be of interest, as indigenous herbivores can response quickly to seasonal changes in forage availability (Skarpe 1991).

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7.2. Internet sources

BIOTA Southern Africa:

www.biota-africa.org (accessed 15th March 2015)

Tropical Rainfall Measuring Mission (TRMM):

<http://trmm.gsfc.nasa.gov/> (accessed 15th March 2015)

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9. DECLARATION - ERKLÄRUNG

Hereby I declare that I have authored this thesis independently, that I have not used other than the declared resources –particularly no internet sources apart from those given as references- and that this thesis has not been submitted before for any degree or examination. The submitted print version is equal to the one on the electronic storage medium. I agree that the master's thesis will be published.

Hiermit bestätige ich, dass die vorliegende Arbeit von mir selbständig verfasst wurde und ich keine anderen als die angegebenen Hilfsmittel -insbesondere keine im Quellenverzeichnis nicht benannten Internet-Quellen- benutzt habe und die Arbeit von mir vorher nicht einem anderen Prüfungsverfahren eingereicht wurde. Die eingereichte schriftliche Fassung entspricht der auf dem elektronischen Speichermedium. Ich bin damit einverstanden, dass die Masterarbeit veröffentlicht wird.

Hamburg, 31th March 2015

Kathrin Schwarz

10. APPENDIX

10.1. Coordinates of vegetation relevés

Table 9: Coordinates of plots. Plot size: 10 m x 10 m. For the Observatory plots, center coordinates of southern line are given. For all other plots, coordinates of north-west corner are given. *) Exact coordinates of plot were lost.

Plot number	Plot number (interim)	Date of recording	Site	Latitude	Longitude
19476	2	20130530	Observatory	-21.5973139	16.9385111
19478	3	20130601	Observatory	-21.5982167	16.9375500
19480	11	20130609	Observatory	-21.5991194	16.9356194
19483	8	20130609	Observatory	-21.5991194	16.9365833
19485	1	20130527	Observatory	-21.5991194	16.9414028
19487	20	20130616	Observatory	-21.6000222	16.9375500
19489	6	20130615	Observatory	-21.6000222	16.9414028
19491	7	20130615	Observatory	-21.600925	16.9394750
19493	15	20130615	Observatory	-21.600925	16.9414028
19495	10	20130610	Observatory	-21.600925	16.9442945
19497	12	20130616	Observatory	-21.6018278	16.9375500
19500	19	20130616	Observatory	-21.6027306	16.9365834
19502	18	20130614	Observatory	-21.6027306	16.9433333
19504	9	20130614	Observatory	-21.6027306	16.9442945
19506	4	20130604	Observatory	-21.6036333	16.9375500
19508	17	20130613	Observatory	-21.6036333	16.9423667
19510	5	20130605	Observatory	-21.6045361	16.9365833
19512	16	20130608	Observatory	-21.6045361	16.9375500
19514	13	20130608	Observatory	-21.6045361	16.9385111
19516	14	20130613	Observatory	-21.6054389	16.9433333

Plot number	Plot number (interim)	Date of recording	Site	Latitude	Longitude
26201	21	20130619	Rehab	-21.6424905	16.9183112
26202	22	20130620	Rehab	-21.642515	16.9188224
26203	23	20130622	Rehab	-21.6426637	16.9197194
26204	24	20130622	Rehab	-21.6430576	16.9201099
26205	25	20130625	Rehab	-21.643xxxx*	19.920xxxx*
26206	26	20130625	Rehab	-21.6433136	16.9206625
26207	27	20130627	Rehab	-21.6436292	16.9211069
26208	28	20130627	Rehab	-21.6437965	16.9215348
26209	29	20130627	Rehab East	-21.6440466	16.9216213
26210	30	20130628	Rehab	-21.6442086	16.9207138
26211	31	20130628	Rehab	-21.6445663	16.9199128
26212	32	20130628	Rehab	-21.6452191	16.9199494
26213	33	20130628	Kudu 2	-21.6046029	16.9138002
26214	34	20130630	Kudu 2	-21.6043874	16.9131857
26215	35	20130630	Kudu 2	-21.6039966	16.9127166
26216	36	20130630	Kudu 2	-21.6035632	16.9119893
26217	37	20130701	Kudu 2	-21.6031058	16.9113905
26218	38	20130701	Kudu 2	-21.6021705	16.9171499
26219	39	20130701	Kudu 2	-21.6014628	16.9163221
26220	40	20130702	Kudu 2	-21.6010738	16.9154278
26221	41	20130702	Kudu 2	-21.6006688	16.9149325
26222	42	20130702	Kudu 2	-21.6036383	16.9149456
26223	43	20130703	Kudu 2	-21.6031157	16.914364
26224	44	20130703	Kudu 2	-21.6027805	16.9137578

Plot number	Plot number (interim)	Date of recording	Site	Latitude	Longitude
26225	45	20130705	Rehab	-21.6445709	16.9181746
26226	46	20130705	Rehab East	-21.6444533	16.9222144
26227	47	20130706	Rehab East	-21.6459838	16.9233286
26228	48	20130706	Rehab East	-21.6464574	16.9240966
26229	49	20130706	Rehab East	-21.6469910	16.9246297
26230	50	20130707	Rehab East	-21.6472908	16.9254853
26231	51	20130707	Rehab East	-21.6478176	16.9262667
26232	52	20130707	Rehab East	-21.6484772	16.9270748
26233	53	20130708	Rehab East	-21.6465322	16.9219902
26234	54	20130708	Rehab East	-21.647059	16.9213404
26235	55	20130708	Rehab East	-21.648335	16.9201886
26236	56	20130709	Rehab East	-21.648012	16.9193720

10.2. Vegetation relevés – cover values

Table 10: Cover values [%] of thorn shrubs and perennial grasses in 2013. Plot size: 10 m x 10 m.

Plot number	Site	<i>Acacia hebeclada</i>	<i>Acacia mellifera</i>	<i>Acacia luederitzii/reficiens</i>	<i>Acacia tortilis</i>	<i>Dichrostachys cinerea</i>	Poaceae annual	Poaceae perennial
19476	Observatory			0.51		1.5		10
19478	Observatory	12.5	1.5	0.16		0.1		12.5
19480	Observatory	0.01	33	0.5				3
19483	Observatory		2	13				28
19485	Observatory		12	2.5	0.1			10
19487	Observatory		4	5				50
19489	Observatory	0.05	35	1.51				30
19491	Observatory		2.5	0.2				25
19493	Observatory		2	2.05		0.5		15
19495	Observatory		2	0.02				12.5
19497	Observatory		1	3.5				30
19500	Observatory	1.5	15	4.05			35	
19502	Observatory		25					25
19504	Observatory		0.01	0.2		1.5		30
19506	Observatory		5	3.06	10			12.5
19508	Observatory	2	30	0.01		1.5		25
19510	Observatory	0.5	12	0.51				5
19512	Observatory		30	0.21	3		5	
19514	Observatory	1	9	2.01	0.6			20
19516	Observatory	12	1.5	0.52		0.1		12

Plot number	Site	<i>Acacia hebeclada</i>	<i>Acacia mellifera</i>	<i>Acacia luederitzii/reficiens</i>	<i>Acacia tortilis</i>	<i>Dichrostachys cinerea</i>	Poaceae annual	Poaceae perennial
26201	Rehab		0.1	0.01		1		20
26202	Rehab	0.01	2			0.5		4
26203	Rehab		0.5					2.5
26204	Rehab		0.1	0.21		0.2		5
26205	Rehab	1	0.1			0.2	10	
26206	Rehab		0.05			0.05		25
26207	Rehab		25					60
26208	Rehab	0.01	18			0.01		45
26209	Rehab East		0.5	0.01		2.5		40
26210	Rehab		0.05	0.05		0.5		50
26211	Rehab		0.01			0.05		25
26212	Rehab		0.2			1.5		36
26213	Kudu 2			0.15	0.1			40
26214	Kudu 2			0.01	0.1			40
26215	Kudu 2		0.05	0.05	40			35
26216	Kudu 2		1		0.05			45
26217	Kudu 2		0.01	0.15	0.1			30
26218	Kudu 2		0.05	0.05	0.2			30
26219	Kudu 2		0.05		0.2			25
26220	Kudu 2		0.05	0.05	25.5			45
26221	Kudu 2				0.2			20
26222	Kudu 2		0.05	0.5	1			30
26223	Kudu 2		0.05					40
26224	Kudu 2		0.01		0.2			25
26225	Rehab		0.1			0.5		15

Plot number	Site	<i>Acacia hebeclada</i>	<i>Acacia mellifera</i>	<i>Acacia luederitzii/reficiens</i>	<i>Acacia tortilis</i>	<i>Dichrostachys cinerea</i>	Poaceae annual	Poaceae perennial
26226	Rehab East		0.2					35
26227	Rehab East		12			1.5		33
26228	Rehab East			0.1		2		20
26229	Rehab East		2			1		15
26230	Rehab East	15	20	0.01		1.5		17
26231	Rehab East	25	0.2	0.01		1.5		30
26232	Rehab East		0.1	0.3	45	2		12
26233	Rehab East		0.75	0.1		1		35
26234	Rehab East		3	2		2		10
26235	Rehab East	2	12	0.15		0.2		6
26236	Rehab East		0.1		0.1	2		9

10.3. Thorn shrub numbers

Table 11: Thorn shrub individual numbers in 2013. Plot size: 10 m x 10 m.

Plot number	Site	<i>Acacia hebeclada</i>	<i>Acacia luederitzii/reficiens</i>	<i>Acacia mellifera</i>	<i>Acacia tortilis</i>	<i>Dichrostachys cinerea</i>
19476	Observatory		3	4		1
19478	Observatory	1	6	54		1
19480	Observatory	1	5	25		
19483	Observatory		169	26		
19485	Observatory		10	3	2	
19487	Observatory		20	10		
19489	Observatory	1	3	6		
19491	Observatory		1	3		
19493	Observatory		7	3		1
19495	Observatory		2	5		
19497	Observatory		17	16		
19500	Observatory	2	4	10		
19502	Observatory			11		
19504	Observatory		3	1		2
19506	Observatory		9	7	5	
19508	Observatory	1	1	4		3
19510	Observatory	2	5	12		
19512	Observatory		3	5	1	
19514	Observatory	3	13	2	2	
19516	Observatory	1	5	2		1

Plot number	Site	<i>Acacia hebeclada</i>	<i>Acacia luederitzii/reficiens</i>	<i>Acacia mellifera</i>	<i>Acacia tortilis</i>	<i>Dichrostachys cinerea</i>
26201	Rehab		1	4		8
26202	Rehab			46		3
26203	Rehab			2		
26204	Rehab		2	1		2
26205	Rehab	1		2		2
26206	Rehab			1		1
26207	Rehab			4		
26208	Rehab	1		4		1
26209	Rehab East		1	1		3
26210	Rehab		1	1		2
26211	Rehab			1		2
26212	Rehab			3		6
26213	Kudu 2		6		5	
26214	Kudu 2		1		3	
26215	Kudu 2		6	2	3	
26216	Kudu 2			29	2	
26217	Kudu 2		3	1	2	
26218	Kudu 2		2	2	3	
26219	Kudu 2			1	3	
26220	Kudu 2		1	2	6	
26221	Kudu 2				4	
26222	Kudu 2		2	1	5	
26223	Kudu 2			1		
26224	Kudu 2			1	5	
26225	Rehab			2		5

Plot number	Site	<i>Acacia hebeclada</i>	<i>Acacia luederitzii/reficiens</i>	<i>Acacia mellifera</i>	<i>Acacia tortilis</i>	<i>Dichrostachys cinerea</i>
26226	Rehab East			4		
26227	Rehab East			3		2
26228	Rehab East		1			10
26229	Rehab East			2		1
26230	Rehab East	1	1	4		6
26231	Rehab East	2	1	3		4
26232	Rehab East		2	5	1	3
26233	Rehab East		5	2		4
26234	Rehab East		1	9		8
26235	Rehab East	2	4	7		1
26236	Rehab East			3	2	5

10.1. Pellet counts

Table 12: Number of pellet groups per plot. Sums of the cross shaped transects (2 x 100 m) are given for each plot.

Plot number	Cattle	Oryx	Kudu	Warthog	Unknown	Site
19476	2	7	0	0	22	Observatory
19478	8	5	1	0	17	Observatory
19480	2	6	0	3	3	Observatory
19483	1	2	0	1	3	Observatory
19485	2	0	0	0	23	Observatory
19487	1	1	0	0	0	Observatory
19489	0	5	1	13	8	Observatory
19491	2	9	0	6	6	Observatory
19493	0	7	0	4	14	Observatory
19495	0	8	0	6	6	Observatory
19497	1	7	0	4	2	Observatory
19500	7	1	0	2	4	Observatory
19502	0	3	3	2	4	Observatory
19504	0	11	0	3	12	Observatory
19506	2	4	0	0	16	Observatory
19508	0	2	0	1	7	Observatory
19510	4	8	3	5	10	Observatory
19512	1	9	0	2	2	Observatory
19514	0	6	0	8	7	Observatory
19516	2	10	0	2	7	Observatory
26201	0	8	0	4	7	Rehab
26202	0	6	3	6	4	Rehab
26203	0	2	4	3	5	Rehab
26204	0	2	1	4	5	Rehab
26205	0	2	0	3	4	Rehab
26206	0	0	1	1	5	Rehab
26207	0	1	1	9	6	Rehab
26208	0	2	2	10	3	Rehab
26209	0	2	1	11	2	Rehab East
26210	0	7	0	12	3	Rehab
26211	0	3	1	6	5	Rehab
26212	0	1	0	12	3	Rehab
26213	0	1	2	9	1	Kudu 2
26214	0	0	1	14	5	Kudu 2
26215	0	0	1	9	6	Kudu 2

Plot number	Cattle	Oryx	Kudu	Warthog	Unknown	Site
26216	0	0	1	4	0	Kudu 2
26217	0	0	1	11	2	Kudu 2
26218	0	1	1	19	0	Kudu 2
26219	0	0	0	10	0	Kudu 2
26220	0	3	2	32	4	Kudu 2
26221	0	0	0	18	2	Kudu 2
26222	0	0	0	9	1	Kudu 2
26223	0	0	0	12	2	Kudu 2
26224	0	0	0	17	3	Kudu 2
26225	0	6	3	10	0	Rehab
26226	0	0	1	9	0	Rehab East
26227	0	3	1	3	2	Rehab East
26228	0	0	3	5	4	Rehab East
26229	0	0	3	6	0	Rehab East
26230	0	1	2	11	4	Rehab East
26231	0	0	3	3	5	Rehab East
26232	0	1	2	6	1	Rehab East
26233	0	1	0	8	3	Rehab East
26234	0	0	3	10	8	Rehab East
26235	0	1	2	10	5	Rehab East
26236	0	0	0	13	6	Rehab East

10.2. Plant reference samples

Table 13: Plant reference species for analysis of fecal samples and stomach content, in alphabetical order.

Species	Family
<i>Acacia erioloba</i>	Fabaceae
<i>Acacia erubescens</i>	Fabaceae
<i>Acacia hebeclada</i>	Fabaceae
<i>Acacia luederitzii</i>	Fabaceae
<i>Acacia mellifera</i>	Fabaceae
<i>Acacia Senegal</i>	Fabaceae
<i>Acacia tortilis</i>	Fabaceae
<i>Albizia anthelmintica</i>	Fabaceae
<i>Aristida congesta</i>	Poaceae
<i>Boscia albitrunca</i>	Capparaceae
<i>Catophractes alexandri</i>	Bignoniaceae
<i>Cenchrus ciliaris</i>	Poaceae
<i>Chloris virgata</i>	Poaceae
<i>Dichrostachys cinerea</i>	Fabaceae
<i>Enneapogon cenchroides</i>	Poaceae
<i>Eragrostis rigidior</i>	Poaceae
<i>Evolvulus alsinoides</i>	Convolvulaceae
<i>Grewia flava</i>	Tiliaceae
<i>Leucosphaera bainesii</i>	Amaranthaceae
<i>Monechma genistifolium</i>	Acanthaceae
<i>Ocimum americanum</i>	Lamiaceae
<i>Otoptera burchelli</i>	Fabaceae
<i>Pollichia campestris</i>	Caryophyllaceae
<i>Stipagrostis uniplumis</i>	Poaceae
<i>Ziziphus mucronata</i>	Rhamnaceae

10.3. Fecal samples

Table 14: Fecal samples, overview.

Species: Oryx

Sample number	Date	Fragments				
		Undetermined	Dicot fragments	Dicot fragments (woody)	Poaceae sp.	<i>Leucosphaera bainesii</i>
F11	20130606	76	70	2	53	7
F12	20130606	66	52	1	31	8
F23	20130608	37	59	0	37	1
F26	20130610	98	59	2	17	1
F29	20130610	72	64	0	78	8
F32	20130610	96	30	0	44	37
F33	20130610	98	24	0	46	21
F34	20130612	105	51	0	18	0
F37	20130615	61	20	0	30	3
F40	20130619	103	54	2	101	18
F41	20130621	72	36	2	15	51
F43	20130621	112	70	3	23	7
F49	20130626	76	109	3	20	20
F52	20130626	72	57	1	14	6
F27	20130610	88	84	1	8	0
n=15						
mean:		82	56	1	36	13

Species: Greater kudu

Sample number	Date	Fragments				
		Undetermined	Dicot fragments	Dicot fragments (woody)	Poaceae sp.	<i>Leucosphaera bainesii</i>
F01	20130527	142	122	4	5	0
F14	20130607	82	100	10	1	0
F15	20130607	37	70	6	0	0
F18	20130607	21	92	8	0	0
F19	20130607	11	132	5	0	0
F20	20130607	67	174	5	0	0
F31	20130610	61	145	11	0	0
F35	20130612	34	138	16	0	1
F44	20130626	38	125	8	0	0
F45	20130626	18	108	2	0	0
F46	20130626	32	179	2	1	0
F47	20130626	61	173	3	0	0
F48	20130626	59	166	4	0	0
F51	20130626	38	155	5	0	0
F71	20130628	48	117	2	0	0
n=15						
mean:		50	133	6	0	0

Species: Cattle

Fragments						
Sample number	Date	Undetermined	Dicot fragments	Dicot fragments (woody)	Poaceae sp.	<i>Leucosphaera bainesii</i>
F04	20130606	90	35	0	93	0
F05	20130606	91	37	1	81	8
F09	20130606	57	21	0	91	0
F22	20130608	62	10	0	51	5
F25	20130609	86	17	0	106	2
F30	20130610	54	16	0	39	3
F61	20130628	76	7	0	109	1
F62	20130628	67	5	0	99	1
F63	20130628	67	7	0	114	1
F64	20130628	34	4	0	71	0
F65	20130628	69	11	2	114	2
F66	20130628	67	24	1	64	0
F67	20130628	40	25	0	63	0
F68	20130628	48	18	0	38	0
F69	20130628	56	18	0	90	0
F70	20130628	78	7	0	73	1
n=16						
mean:		65	16	0	81	2

Species: Warthog

Fragments						
Sample number	Date	Undetermined	Dicot fragments	Dicot fragments (woody)	Poaceae sp.	<i>Leucosphaera bainesii</i>
F02	20130606	54	6	0	54	0
F03	20130606	50	3	0	112	0
F06	20130606	29	0	0	91	0
F10	20130606	43	7	0	105	0
F13	20130607	15	2	0	69	0
F24	20130608	34	0	0	122	0
F36	20130612	33	1	0	78	0
F38	20130619	41	3	0	69	0
F39	20130619	38	3	0	132	0
F50	20130626	57	2	0	111	0
F53	20130626	60	1	0	88	0
F54	20130626	68	5	0	65	0
F55	20130627	45	2	0	118	0
F56	20130627	59	1	0	108	0
F59	20130628	30	0	0	141	0
F60	20130628	32	0	0	70	0
n=16						
mean:		43	2	0	96	0

10.4. Stomach content samples

Table 15: Stomach content samples, overview.

Sample number	Species	Locality	Date	Fragments			
				Undetermined	Dicot fragments (woody)	Dicot fragments (not woody)	Poaceae sp.
M1	Cattle	Hüttenhain	20130529	9	1	5	105
M2	Oryx	Erichsfelde	20130610	6	0	4	110
M3	Oryx	Erichsfelde	20130623	18	5	11	86
M4	Oryx	Erichsfelde	20130623	15	12	3	90
M5	Oryx	Erichsfelde	20130623	20	3	10	87
M6	Warthog	Erichsfelde	20130626	3	0	0	117
M7	Oryx	Erichsfelde	20130630	19	2	9	90
M8	Oryx	Erichsfelde	20130711	15	2	11	92
M9	Oryx	Erichsfelde	20130713	18	10	7	85