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## Effects of elephants and other browsers on woody vegetation around artificial waterholes in Savuti, northern Botswana



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## Abstract

On dry African savannas permanent water bodies are very important to both wildlife and vegetation, and especially so during the dry season. Water dependant animals gather around waterholes and impose heavy browsing pressure on adjacent vegetation. Because of increasing animal abundances, a fear that has been raised is the loss of woody vegetation and trees around such natural water points. In an attempt to relax the browsing pressure around natural waters, artificial waterholes have been built in some southern African game conservation areas. Of course constructing new permanent water stations in an arid area will alter the vegetation communities of the area and the magnitude and direction of these changes are vital to the understanding and evaluation of the future of plant species in such an area. Plants responds to herbivory by generally one out of two strategies, resistance and tolerance to herbivory, *i.e.* either by defending itself from tissue losses or by compensating the loss by fast or substantial regrowth. Which one of these strategies that is most beneficial in an area is thought to depend on the nutritional state of the soil. This study aims to evaluate the changes in woody vegetation around two artificial waterholes in Chobe, Botswana and to try to enhance the understanding of the two herbivory related strategies and how they affect these vegetation changes. Complete records on woody plants were recorded for 32 plots divided on 4 transects starting from the waterhole and stretching out in the surrounding vegetation. Plant functional traits such as spine sizes and densities and leaf sizes were sampled and information on chemical properties of the plant species was used from previous studies. Using multivariate methods of ordinations I found that during five years the woody vegetation had indeed changed and areas closest to the water have changed considerably more than further away. I have found evidences that soil types are important for the stability, vegetation dynamics, and for the presence of resistance and tolerance in the plants. I have also found that some of the most common species in the area have the ability to respond to herbivory by tolerance traits such as increasing leaf and leaflet sizes.

## Introduction

Plant responses to herbivory and resource limitations are of key importance in understanding vegetation changes and consequences of human impacts in a natural landscape and perhaps especially so in water limited, herbivore rich wildlife concentration areas. Two general strategies by which plants respond to herbivory have been suggested, that of resistance and that of tolerance to herbivory (Strauss & Agrawal 1999). Chemical defence compounds and morphological defences like spines and hooks are commonly found examples of plant resistance to herbivory, to minimize damage to the biomass (Stamp 2003). Tolerance on the other hand is a plant's ability to endure herbivory, *e.g.* by fast and/or sizable regrowth after being browsed. This can be done by coppicing, the production of greater numbers of new shoots, or by increasing leaf or shoot sizes (Skarpe & Hester 2008).

The relative viability of the two herbivory related strategies, resistance and tolerance, has been thought to depend on the intensity of browsing and the resource availability of the soils (Coley *et al.* 1985). Slow growing plants adapted to nutrient poor soils are believed to benefit from investing in quantitative chemical defences (carbon-based substances, phenols and tannins), spines and other resistance traits (Coley *et al.* 1985). On the other hand, fast growing species adapted to nutrient rich soils rather invest in tolerance traits such as coppicing and, under very heavy herbivory, low concentrations of carbon-cheap qualitative defences (Coley 1983, Coley *et al.* 1985, Herms & Mattson 1992). The logic behind the theory is explained by Coley *et al.* (1985) in three parts: Where resources are limited the value of nutrients is greater, thus increasing the cost of replacing lost tissues. Therefore avoiding herbivory becomes important and is why plants on poor soils should invest in defences. Furthermore, at a lower growth rate the yearly production is smaller. So at a given browsing intensity, a slow growing species will lose a larger part of the total production than plants with a higher growth rate, which of course makes defences more important for slow growers. Thirdly, as the costs of defences must be proportional to the amount of tissue that needs protection, defences rapidly become more expensive for fast growing than for slower growing species.

However, evidence for the theory of herbivory related strategies being dependent on soil nutrients has been contradictory. Rooke *et al.* (2004) found that *Colophospermum mopane*, a common slow growing tree species in the northern parts of southern Africa utilized by elephants and other browsers (Ben-Shahar 1993), responds to browsing by tolerance as well as being chemically defended, something that goes against the original theory of slow growing species that are adapted to nutrient poor environments should be investing in resistance exclusively. The two strategies can function simultaneously in one plant species (Fornara & du Toit 2007), and must not necessarily be mutually exclusive (Mauricio *et al.* 1997). Hrabar *et al.* (2009) for example, found that *C. mopane* did not show any trade-off between the investment in regrowth and chemical defences.

In contrast to constitutive defences, inducible defences are not always present in a plant but are activated by certain cues from the surrounding environment (Skarpe & Hester 2008). Inducible defences have the advantage of being costly for the individual plant only when needed, which may be an advantageous tactic in a highly disturbed area (Stamp 2003). All sorts of defences can be inducible, morphological as well as chemical (Gowda 1997, Stamp 2003). Evidence of induced spinescence in response to increased herbivory has been studied mainly in *Acacia* species on the African savannas (*e.g.* Young 1987, Gowda 1997 and Rohner & Ward 1997). Increased spinescence can manifest itself as the increase in spine lengths (Young 1987, Rohner & Ward 1997) and/or spine density (Rohner & Ward 1997). Spines offer the defence from herbivores in terms of limitation of bite sizes. By dividing shoots into smaller segments, spines prevent leaf stripping and limit the bite sizes of browsing herbivores (Cooper & Owen-Smith 1986, Wilson & Kerley 2003). Hereby the intake rate of a browsing herbivore is reduced (Cooper & Owen-Smith 1986), and the spinescent plant will lose less biomass compared to a corresponding plant without spines.

As for tolerance, compensatory regrowth has been recorded in several common African woody species, e.g. *Combretum apiculatum* (Bergström *et al.* 2000), *Acacia erubescens* (Dangerfield & Modukanele 1996), *Acacia tortilis*, *Colophospermum mopane*, *Grewia flava*, *Peltophorum africanum* and *Ziziphus mucronata* (Rooke *et al.* 2004). Tolerance ability may be displayed by the increase of shoot and/or leaf sizes (Rooke *et al.* 2004, Hrabar *et al.* 2009) or density of new shoots (Rooke *et al.* 2004). Increased leaf or shoot sizes can reduce herbivore attacks by offering bite sizes greater than the bite diameter of the herbivore, thus making feeding ineffective (Wilson & Kerley 2003, Makhabu *et al.* 2006b). Furthermore, by allocating more resources to producing more photosynthetic tissue, the plant can faster compensate for lost organic matter and restore its photosynthetic capacity (Skarpe & Hester 2008).

The composition of herbivore communities exploiting a water source will be affected by the strategy by which surrounding plants respond to herbivory. The vigorous regrowth in tolerant plant species, triggered by the browsing of elephants and other large herbivores, is associated with an increased palatability of new shoots and therefore further usage by herbivores of the same or other species is promoted (Jachmann & Bell 1985, du Toit *et al.* 1990, Styles & Skinner 2000, Makhabu *et al.* 2006a). Browsers are known to prefer previously browsed *C. mopane* and other tolerant trees from those that have not been browsed in the past by e.g. elephants (du Toit *et al.* 1990, Bergström *et al.* 2000, Smallie & O'Connor 2000, Makhabu *et al.* 2006a), and by this positive feedback mechanism heavily browsed, intensely resprouting trees may form a so called “browsing lawn” that favour the continued usage by herbivores (Styles & Skinner 2000, Makhabu *et al.* 2006a, Fornara & du Toit 2007).

In arid zones, elephants and other water dependent browsers spread out over large areas during the rainy season when water is abundant to reduce inter- and intraspecific competition (Ben-Shahar 1993) and will thus have a small and more even impact on the vegetation during this period. However, in the dry season, animals congregate around the water resources, which will impose a strong browsing pressure on the surrounding vegetation (Skarpe *et al.* 2004). A pattern of decreasing browsing pressure with distance from a waterhole is one factor that has been found around waterholes, as well as the creation of a “sacrifice area” of complete vegetation loss at the closest vicinity of water, partly derived from the heavy trampling by game (Brits *et al.* 2002, Todd 2006, Epaphras *et al.* 2008, Chamaillé-Jammes *et al.* 2009).

Preventing undesired vegetation alterations, both in structure and species compositions, maintaining biodiversity and a heterogeneous landscape and preventing vegetation loss around permanent waters – these are of concern to managers of wildlife concentration areas as well as for the safari tourism (Ben-Shahar 1996, Skarpe *et al.* 2004). It has sometimes been dealt with by culling elephants in an attempt to limit vegetation damage by controlling elephant population numbers (Barnes 1983, Young *et al.* 2009). Elephants are large-impact animals that can alter whole landscapes. They are believed to be primarily responsible for clearing the landscape by reducing bush and tree density in areas where they are abundant (Barnes 1983, Guldemond & van Aarde 2008). This is however usually a result of the combined effects of elephants and smaller browsers and/or fire, with elephants enhancing the mortality of larger trees and smaller browsers and/or fire preventing the survival of seedlings (Belsky 1984, Prins & van der Jeugd 1993, Moe *et al.* 2009). Elephants alone are therefore not responsible for vegetation changes and for this reason, among others, the effectiveness of the culling approach has been much debated (Skarpe *et al.* 2004, Guldemond & van Aarde 2008, Young *et al.* 2009). Another approach is to supply water in additional locations during the dry season to lessen the browsing/grazing pressure around the permanent water sources.

Chobe National Park in Northern Botswana houses an elephant population of around 70 000 individuals (Dipotso 2005), part of a large continuous free ranging population consisting of about

one third of all African elephants (van Aarde & Jackson 2007). To protect the vegetation from over-utilization without having to cull and thus maintaining the elephant population at such great numbers, the Department of Wildlife and National Parks (DWNP) of Botswana and Chobe park management decided to build artificial watering points in the park in the early 1990's (Dipotso 2005). By providing extra watering points in the dry season, they argued that the browsing pressure on the vegetation around the natural permanent waters (such as the Chobe riverfront) would be less destructive (supported by findings of *e.g.* Epaphras *et al* 2008) and spreading the elephant population on a bigger area would simplify animal viewings and minimize disturbance by tourism in the park (Barnes 1983, Dipotso 2005).

Ecologists have on the contrary been pushing the point that when providing water in more places, although the local elephant densities will decrease at first, when animals spread out more evenly over a larger area, the elephants will eventually multiply until they reach the new carrying capacity decided by the water availability of the area (O'Connor *et al* 2007). If elephants are spread out over a larger part of a protected area, the overall biodiversity of this area may decrease since the intensity and mode of browsing becomes more homogeneous throughout the landscape which will affect woody plant species differently and species that do not support elephant presence may be lost. In addition, the strong effects on vegetation along gradients out from watering points in animal rich-water limited areas are natural phenomena that have probably existed in this way for thousands of years (Skarpe *et al.* 2004). So instead of solving the problem, provision of additional watering points may lead to more widespread problems in the future.

Regardless of the reason for building them, artificial watering points will undeniably have strong effects on the adjacent vegetation where they are built. Some studies have been performed in areas of artificial watering points (*e.g.* Thrash 1998, Brits *et al.* 2002 and Epaphras 2008, Kalwij *et al.* 2010) and usually a vegetation loss at the vicinity of the water is observed, although Kalwij *et al.* (2010) contradictorily found an actual increase of tree density around such artificial watering points. Additionally, because browsing is selective between woody species and because plant herbivore defence can have varied efficiency towards different herbivore species, increased herbivore densities may cause changes in plant species composition (Guldmond & van Aarde 2007, Skarpe & Hester 2008). Thus provision of additional water during the dry season is a controversial deed and the effectiveness and long-term effects thereof are under debate (Owen-Smith 1996, Skarpe *et al.* 2004).

The objective of this study is to investigate the temporal and spatial variation in woody vegetation around artificial watering points and into the surrounding dry savanna in semi-arid Chobe National Park in northern Botswana. In concurrence with earlier studies I expect to find a gradient in browsing pressure by elephants and ruminant browsers diminishing with distance from the watering points. The study is based on the following questions:

Does the composition of woody vegetation vary in time and space around the artificial waterholes?

- a. If so, how does the variation relate to differences in browsing intensity and soil conditions (resource availability)?
- b. Can the variation in species composition be explained by plant herbivory-related strategies as expressed by species-specific traits related to tolerance or to resistance?
- c. Is there an intraspecific variation in herbivory-related plant traits with distance to water points?

## Materials and methods

### *Study area*

The Chobe National Park is situated in the north of Botswana, bordering to Namibia by the Chobe River. It was declared a national park in 1967 (although it was proposed already in 1931) and covers an area of 10 566 km<sup>2</sup> (Botswana Tourism Board 2006a). The climate is sub-humid with a mean annual precipitation in the far north of 650 mm (Botswana Tourism Board 2006b). The climate is strongly seasonal with the rainy summer season stretching from October to April and the dry winter season with close to no rain, from May to September (Botswana Tourism Board 2006b). Temperatures range from an average maximum of 39°C in October (warmest month) to an average minimum of 4°C in July (coldest month; Botswana Meteorological Services; unpublished Department records).

The study was conducted in the Savuti area of Chobe National Park from February to April 2009. The Savuti landscape consists of grass plains situated on alluvial soils attesting of what used to be part of a large lake dominating much of Botswana long ago, and remained as the Savuti Marsh until the late 1800's (Main 1987). These plains are surrounded by and sometimes interrupted by patches of nutrient poor, red Kalahari sands on which woodlands and wooded savannas are found (Main 1987).

Two artificial waterholes were analysed: Rhino vlei and Marabou vlei, constructed in the early 1990's to supply borehole water to animals in the area during the dry season (Dipotso 2005). The waterholes have been used in previous studies of vegetation responses to artificial watering points by Moghohgo (1995, unpublished) and Dipotso (2005), which enables us to study changes in the vegetation in time as well as in space.

### *Data collection*

The woody vegetation around the two artificial waterholes and into the surrounding areas were investigated using two transects per waterhole. Transects in east and west direction were chosen because Marabou vlei is situated south of Rhino vlei and the effect of either one of the waterholes on the vegetation would be less distinguishable in the area between them. Along each transect were 8 sampling plots on distances of 200, 400, 600 800, 1000, 2000, 4000 and 5500 metres from the waterholes. Plots were located by GPS (Table 1). Coordinates for all plots were found by adding or subtracting the correct distances from the east-west coordinate of a position taken at the waterhole. The plot coordinates thus calculated refer to the southwestern corner of the plots. Plots are identified by the initials of the waterhole (M for Marabou vlei, R for Rhino vlei), and the cardinal direction of the transect (E for east, W for west) together with the distance of the plot from the waterhole (so, ME600 is the plot 600 m from Marabou vlei along the eastern transect). Each plot was 50x50 m and was delineated using tape measures.

Table 1. GPS locations for the southwest corner of all plots analysed in 2009.

	Water-hole	200 m	400 m	600 m	800 m	1000 m	2000 m	4000 m	5500 m	
<b>Marabou vlei East</b>	Y	0097675	0097505 <sup>a</sup>	0097275	0097075	0096865 <sup>b</sup>	0096675	0095675	0093675	0092175
	X	2066496	2066496	2066496	2066496	2066486 <sup>b</sup>	2066496	2066496	2066496	2066496
<b>Marabou vlei West</b>	Y	0097675	0097875	0098075	0098275	0098475	0098675	0099675	0101675	0103175
	X	2066496	2066496	2066496	2066496	2066496	2066496	2066496	2066496	2066496
<b>Rhino vlei East</b>	Y	0095750	0095550	0095350	0095150	0094950	0094750	0093750	0091750	0090250
	X	2061482	2061482	2061482	2061482	2061482	2061482	2061482	2061482	2061482
<b>Rhino vlei West</b>	Y	0095750	0095950	0096150	0096350	0096550	0096750 <sup>c</sup>	0097750	0099750	0101250
	X	2061482	2061482	2061482	2061482	2061482	2061482 <sup>c</sup>	2061482	2061482	2061482

a = Plot moved 30 m to the west because of car tracks, thus plot placed 170 m from Marabou vlei.

b = Plot moved because of car tracks and therefore placed 810 m east of Marabou vlei.

c = Coordinates for the northeast corner. Plot moved because of car tracks.

A rough classification of soil types was done by eye for each plot using 2 categories: color (white (W), grey (G) or red (R)) and texture of sand (fine (F), intermediate (I) or coarse (C)). The soil categories are designed to give an indication of nutrient content (ranging from white alluvial soil to red nutrient deficient Kalahari sand; Main 1987) and water-holding capabilities (ranging from fine clay-like particles to coarse sand particles).

All woody plant individuals with heights  $\geq 0.2$  m were recorded and identified to species to make a complete record of species and their abundances in the plots (data collected by Skram Vatne 2010). Plant species scientific names are used according to the flora by Coates Palgrave *et al.* (2003). Dead trees were also included and identified when possible. Corresponding abundance data were also collected in 2004 by Dipotso (2005). Dipotso collected woody species abundances at the same two waterholes and transects but with only 7 plots each (200, 400, 600, 800, 1000, 2500 and 4000 m from the waterholes).

All woody plants within the plot that had more than 80% of the canopy between 0.3 and 3.0 m above ground were sampled for plant functional traits. This was to exclude seedlings and trees that were out of browsing reach for most ungulate browsers (except elephant and giraffe). Of species with high densities in a plot, only 10–15 individuals per species were sampled for time reasons. Some traits were sampled as two measurements per individual. This was done to allow the calculation of an average measurement per individual to standardize the variation in the trait naturally found within individual plants. The traits sampled were:



\*Leaf lengths and widths measured in mm, were recorded for two randomly chosen leaves as two perpendicular dimensions at the longest and widest place of the leaf, respectively. As a standardization of leaf size for all trees a leaf size index was calculated as follows:

$$\text{Leaf size Index} = \frac{\text{Leaf length} \times \text{Leaf width}}{2}$$

\*Leaflet lengths and widths were measured for compound leaves in the same way as above and leaflet size index calculated as the leaf size index.

\*Spine and hook length was measured in mm for one spine or hook on two randomly chosen shoots per tree. The spine/hook closest to a point 10 cm from the shoot tip was measured.

\*Spine and hook densities were recorded on two randomly chosen shoots of each spinescent tree. Number of spines and hooks along 10 cm, from shoot tip and inwards, represent the density of spines or hooks.

\*Reproductive traits: Flower buds, flowers, fruits and signs of spread fruit were recorded only as present or absent on the individual. This measurement did not yield enough data and was therefore not included in any analyses.

\*Assessment of recent browsing pressure of the plant as proportion of total number of shoots browsed.

\*Assessment of the accumulated browsing on the plant as a measure of long term browsing impact.

Recent browsing pressure was calculated as the number of browsed new (this year's) shoots divided by the total number of new shoots on the plant. The total number of new shoots were counted on small trees, and on larger trees where shoot counting would be very time consuming, only shoots on part of the canopy was counted and the total number of new shoots estimated from this number. Due to differences in feeding mode and bite diameters, browsing by elephants can in most cases be distinguished from that by ruminants. Independent browsing pressures were therefore recorded for elephants (E br) and ruminants (R br).

The estimation of accumulated browsing pressure (Acc br, how much browsing has affected the plant throughout its life) was done using a scale of 4 categories, 0–3 (0 = no old browsing visible; 1 = old browsing visible but has not affected the growth pattern of the plant; 2 = growth pattern changed because of browsing; 3 = plant growth pattern drastically changed by heavy browsing). Here no distinction can be made between elephant and ruminant impact although it is plausible that most of the accumulated browsing is caused by elephants.

In addition, some information on plant traits was retrieved from the Botswana Tree Database (by Roger Bergström, Christina Skarpe & Kjell Danell, unpublished), including if the species are typically growing as a shrub or a tree, and whether or not they are evergreen or spinescent (for species that did not occur in this study but were collected by Dipotso in 2004). Information about the species' chemical properties and defences (nitrogen (N) and acid detergent fiber (ADF) contents (% of dry mass) and total phenol (TP) and tannin (TT) concentrations (mg tannic acid/g dry mass) in plant parts) were kindly provided by Tuulikki Rooke. Trees displaying chemical defence were further divided into groups according to the typical concentration of chemicals in leaves. Nitrogen, fiber, phenol and tannin concentrations were divided into two groups each representing low and high concentration respectively: N1 (<3.0%), N2 (≥3.0%), ADF1 (<60%), ADF2 (≥60%), TP1 (<50mg TA/g), TP2 (≥50 mg TA/g), TT1 (<100 mg TA/g) and TT2 (≥100 mg TA/g). These groups were used in the t-tests and as explanatory variables in the ordinations.

Since the tolerance to herbivory strategy is not necessarily determined by specific measurable traits that can be collected at a single sampling occasion, I have relied upon measurements of the resistance strategy assuming that, in such a highly disturbed place, plants will be dependant on either one of the two general strategies to cope with the browsing pressure. Thus, whenever resistance could be ruled out but tolerance was not verified, I have assumed that a non-resistant species by default is, in one way or another, a tolerant species.

### *Data analysis*

To investigate the variation in the plots' woody plant community composition in time and space I have been using multivariate statistical models, *i.e.* ordinations. Two general strategies to create ordination graphics are the direct and the indirect gradient analysis. In the direct gradient analysis (including *e.g.* the Canonical Correspondence Analysis (CCA)) only the variation explained by linear combinations of the explanatory variables included in the analysis are taken into account (Lepš & Šmilauer 2003a+b). In the indirect gradient analysis (including the Principal Component Analysis (PCA), Correspondence Analysis (CA) and Detrended Correspondence Analysis (DCA)) samples are distributed in the graphic according to the total variation between samples in the primary data inserted and explanatory variables are added according to best fit on this sample pattern (Lepš & Šmilauer 2003a+b). Both strategies are used in this study to illustrate different aspects of the sampled data.

When deciding between linear (PCA) and unimodal (CA, CCA, DCA) ordination method I followed the general guide presented by Lepš & Šmilauer (2003c). According to this manual a DCA (detrended by segments) can be used to discriminate between the two general methods. If, by this ordination, the longest ordination gradient shows a value above 4.0 standard deviations, a unimodal method will work best. Values below 3.0 indicate that linear methods are preferred, whereas between 3.0 and 4.0 both methods will work satisfactorily. Whenever I obtained a value between 3.0 and 4.0 standard deviations, I chose to use unimodal methods.

It is important to discriminate between three factors in the ordination terminology: sample, species and explanatory (or environmental) variables. Hereafter the definitions by Lepš & Šmilauer (2003a) are used for these terms. Primary data are entered in the ordination software as a species-sample matrix (here sample = plot and the matrix thus holds the recorded abundance of each species for all plots), and explanatory variables are included as an explanatory factor-sample matrix (*e.g.* including environmental variables like the soil types of the plots and plot distances from the water source; Lepš & Šmilauer 2003a). This "normal" set-up can be modified to reveal different aspects of the recorded data. For example, plant characteristics and browsing pressures can be incorporated as explanatory variables and thus their relation with each other and the species composition can be interpreted.

The software CANOCO for Windows 4.5 was used to create all ordinations. To eliminate the variation caused by differences between the two waterholes, these were included in the ordinations as covariables. Species abundance data were entered as relative abundance (%) and log transformed. For all ordinations, explanatory variables were tested for significance using the Forward Selection procedure in the CCA with the Monte Carlo Permutation Test (499 unrestricted permutations), and only significant (or close to significant) variables were included in the ordinations and biplots. The F values, the significance and  $\lambda$  (the amount of variance in the ordination that could be explained) for the explanatory variables are also calculated in the CCA and were used for interpretation of the data.

To analyse temporal differences in plant species composition data, Dipotso's (2005) species

composition data for east and west transects around Marabou- and Rhino vleis collected in 2004 and Skram Vatnes' data from 2009 were compared using a CA. In an ordination graph, the distance between plots is a measure of their dissimilarity, and therefore the distance between a given 2004 plot and its corresponding 2009 plot can be interpreted as the magnitude and direction of change in species composition at this location during these 5 years. One pair of plots, RW2500 (2004) & RW2000 (2009), were removed from this ordination because they were outliers. The distance from the water source, time of collection (2004 or 2009) and soil types were tested for significance as explanatory variables.

Differences from year 2004 to 2009 in abundances of certain tree species were tested with paired t-test to pinpoint species that have been increasing or decreasing in abundance between surveys. Abundances in all plots from 2004 were compared with abundances in corresponding plots from 2009 for each analysed species separately. The nine most commonly found species were tested in this fashion: *Acacia hebeclada*, *Acacia tortilis*, *Boscia albitrunca*, *Colophospermum mopane*, *Dichrostachys cinerea*, *Diospyros lycoides*, *Grewia schintzii*, *Lonchocarpus capassa* and *Lonchocarpus nelsii*.

The spatial variation in vegetation composition was analysed in a CA using only the abundance data from 2009. Explanatory variables included in the analysis were: soil types and distances from the water source. Two plots, RW600 and RW2000, were excluded from analysis on account of them appearing as outliers in the resulting graph. RW2000 was situated on an open grass plain and contained only 1 tree, whereas RW600 almost exclusively contained *Combretum mossambicense*, a species that occurs only in low numbers in other plots. Clusters of plots found in the CA biplot are plots sharing a typical vegetation type.

Furthermore, a TWINSPLAN (two-way indicator species analysis) was performed and the clusters found by this method were compared with the clusters found in the CA analysis. The Twinspan is a divisive hierarchical classification method that uses a normal CA to order plots according to the abundances of species and the species' respective weight in the dataset as a whole. It will then split the plots into two groups where the abundances of the highest weighted species differ the most (Curtis 2001, Henderson 2006). This procedure is repeated a specified number of times to create new alignments within the subgroups that can be split into smaller and smaller clusters of plots with more and more similar species composition. This analysis was made to compare with the results of the CA and to strengthen these results. The Twinspan analysis was performed using the software WinTwin with 5 cutlevels (0; 0.2; 0.4; 0.6 and 0.8) and 5 levels of divisions.

Trends in browsing pressure and the presence of certain plant traits across species were analysed by Spearman's Rank Correlations, since data did not have normal distribution even after transformation. The correlations between, on the one hand, the different browsing measurements (elephant, ruminant and accumulated browsing pressure), leaf size index, evergreenness and, on the other hand, distance from waterholes were examined. For each species and plot, mean values of these variables were calculated, except for evergreenness that was scored as number of individuals with this characteristic per plot. These values were then used in the Spearman rank correlation analysis to determine if there were correlations between variables across species. All Spearman Rank Correlations were conducted in the interactive tool provided by Wessa (2009).

In the same way as for abundances of tree species earlier, paired t-tests were employed to test differences in numbers of individuals displaying different plant traits in the two collected years. Abundances of plant individuals with the traits in all 2004 plots were paired with the abundances in their corresponding 2009 plot and analysed with the paired t-test. Consequently traits that have increased or decreased in time could be detected. Plant traits analysed were: spinescence, evergreenness, N, TT, TP and ADF. All paired t-tests were performed in the statistical software

Minitab™.

To explain the relationship between herbivory related traits, browsing pressures and environmental factors, a CCA was employed. Abundances of plants displaying different plant traits were scored for all plots in an explanatory factor-sample matrix and used in the CCA. The included explanatory factors were: spinescence, evergreenness, growth form (shrub and/or tree), leaf size index, N, ADF, TP, and TT concentration groups, accumulated, ruminant and elephant browsing pressure, soil types and distance to the water source. Leaf size index was divided into 3 classes, according to increasing size: I1 (<500), I2 (500-5000), I3 (>5000) and the groupings of the chemical properties defined earlier were used here. Elephant, ruminant and accumulated browsing pressures were calculated as averages for each plot. The correlation matrix calculated by the CANOCO package was used as a foundation for interpretation of the graphics and conclusions drawn thereof.

The ability of plants to modify herbivory-related traits phenotypically in accordance to the browsing conditions under which they grow was investigated in an additional set of Spearman Rank Correlations. Intraspecific variation in tolerance (leaf and leaflet sizes) and resistance traits (spine lengths and densities) were correlated with each other and with certain environmental factors such as distance from waterhole and the recorded browsing pressure of elephants (E br) and ruminants (R br) as well as the history of browsing quantified as accumulated browsing (Acc br). All combinations of these variables were analysed for 5 of the most common species: *A. hebeclada*, *B. albitrunca*, *C. mopane*, *L. capassa* and *L. nelsii*. Means of the variables were calculated for the species in each plot and used in the within-species analysis.

## Results

### *Does the composition vary in time and space around the artificial waterholes?*

The plant species compositions around the artificial waterholes have changed during the five years between data collections (Figure 1), but not all plots have changed equally much. Some plots studied show almost no or very small community changes, while others have undergone major alterations and have changed vegetation type. Most of the plots that have undergone substantial change in woody vegetation composition are located  $\leq 1$  km from the waterholes. Indeed, distance from the water source is an environmental factor that significantly explains the distribution pattern ( $F = 2.316$ ;  $p = 0.01$ ) along with differences in soil type WI ( $F = 3.902$ ;  $p = 0.004$ ). Out of the plots situated on the WI soil type, only one had changed notably in species composition between years (Figure 1).

Across plots, only *Acacia hebeclada* has increased in numbers between the two sampling occasions whereas *B. albitrunca* and *Colophospermum mopane* are species that seem to have decreased in the area (Table 3). Moreover, the plots that have not changed much seem mainly to be those containing high densities of *C. mopane* (cluster 4, Figure 1). Plots that have changed in species composition are generally plots with fewer woody individuals and not as completely dominated by *C. mopane* as the unchanged plots (mainly cluster 1 and 2, Figure 1).

The residing plant species compositions were not found to vary in space in relation to the waterhole. A CA ordination analysis on current woody plant communities (2009) showed that distance from the water source is a factor that does not have significant effect on the distribution of woody plant species in the 2009 dataset (Table 4).

Table 2. Acronyms.

<u>Acronyms: (used in figures and tables)</u>	
Ds	Distance from water source
WI	Soil type white/intermediate particles
WF	Soil type white/fine particles
GI	Soil type grey/intermediate particles
GF	Soil type grey/fine particles
Spince	Spinescence
Evergr	Evergreenness
Tree	Growth form typically tree according to the Botswana Tree Database
Shrub	Growth form typically shrub according to the Botswana Tree Database
Acc br	Accumulated browsing pressure
E br	Elephant browsing pressure
R br	Ruminant browsing pressure
TT1-2	Total tannin content groups 1-2 (low-high concentration)
TP1-2	Total phenol content groups 1-2 (low-high concentration)
N1-2	Nitrogen content groups 1-2 (low-high concentration)
ADF1-2	Acid Detergent Fiber content groups 1-2 (low-high concentration)
I1-3	Leaf size index groups 1-3

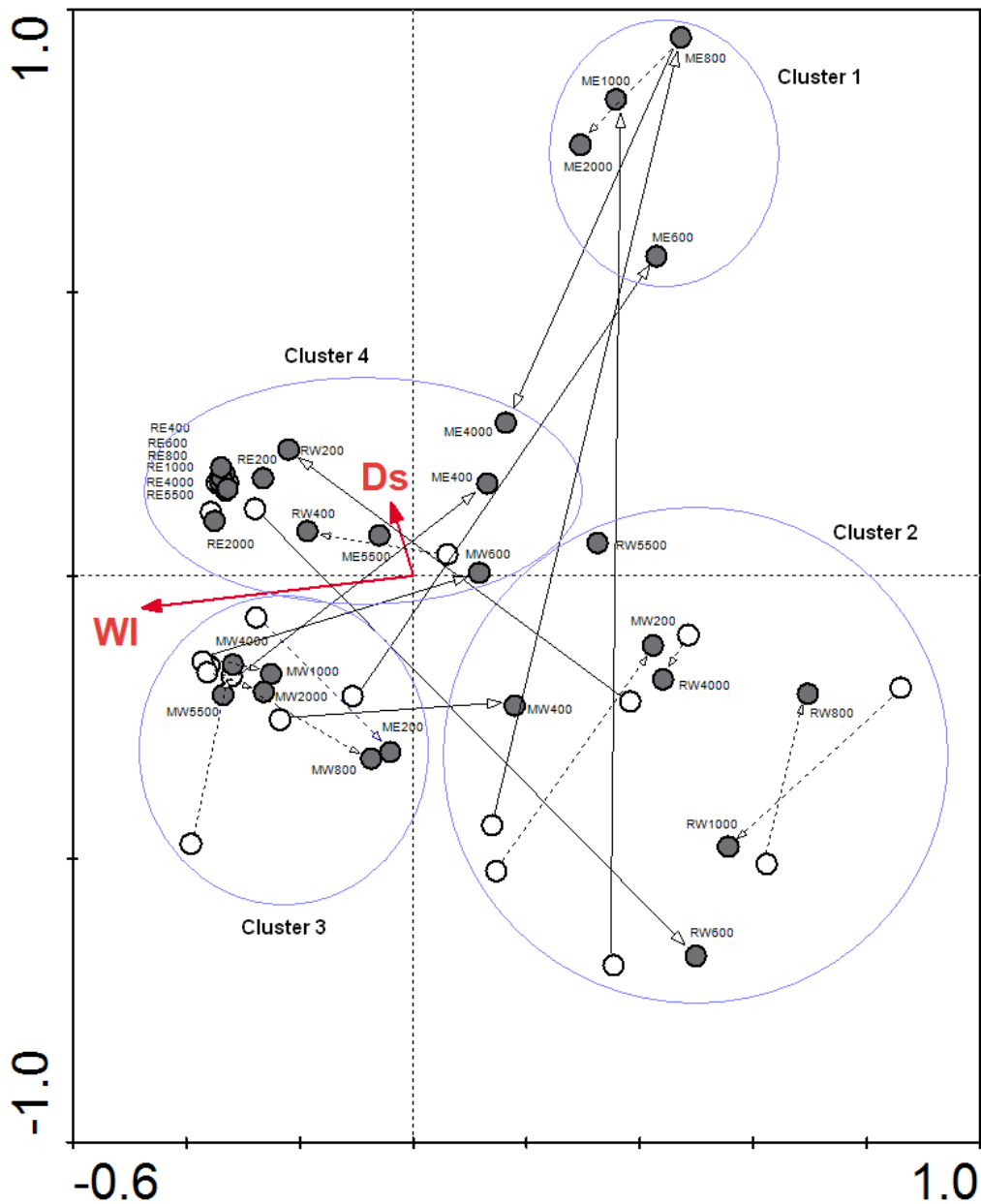


Figure 1. CA ordination of woody vegetation data from 2004 (white circles) and 2009 (grey circles). Only environmental variables with significant effects are included (WI and Ds, acronyms from table 2). Plot names are composed of the first letter in the name of the waterhole (M for Marabou vlei, R for Rhino vlei) and the cardinal direction of the transect (E for east, W for west) together with the distance in m from the waterhole. Clusters 1-4 are the defined clusters from the CA in figure 2. Corresponding plots from 2004 and 2009 are connected with the arrow pointing to the latter. Dotted arrows are for plots that have not changed cluster (vegetation type) and full lined arrows for plots that have. The grey circle for ME800 is obscuring two white circles, ME2000 and ME4000 (2004), which is why three arrows are connecting to this point.

Table 3. Paired t-test on the change of abundances between 2004 and 2009 for 9 species.

Species	t-value	p	n
<i>Acacia hebeclada</i>	4.25	0.0001	28
<i>Boscia albitrunca</i>	-2.21	0.036	28
<i>Colophospermum mopane</i>	-1.87	0.072	28
<i>Grewia schintzii</i>	1.54	0.135	28
<i>Diospyros lycoides</i>	-1.19	0.244	28
<i>Lonchocarpus capassa</i>	0.89	0.382	28
<i>Acacia tortilis</i>	0.85	0.403	28
<i>Dichrostachys cinerea</i>	0.42	0.677	28
<i>Lonchocarpus nelsii</i>	0.42	0.678	28

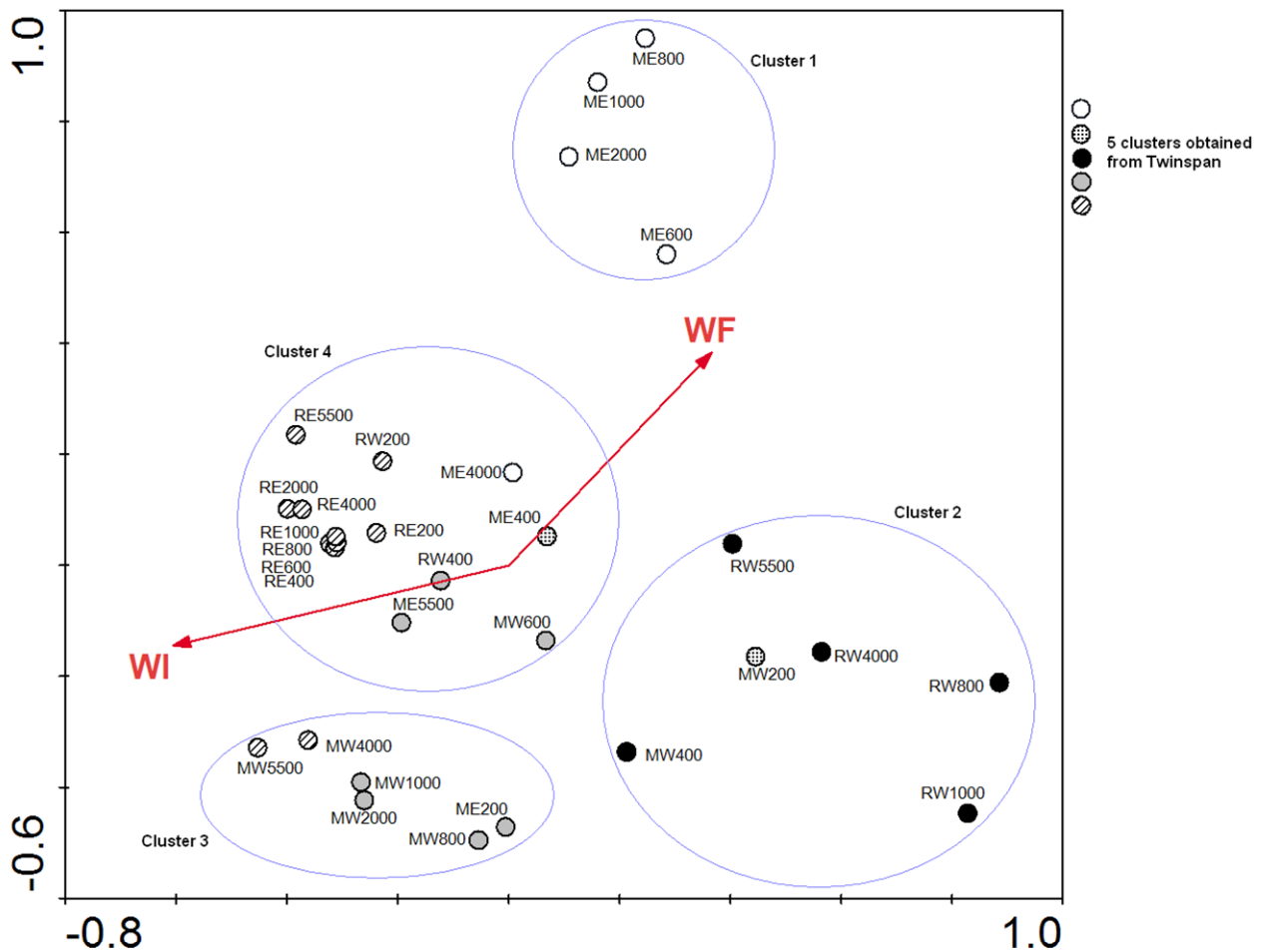


Figure 2. CA ordination of the 2009 plots in relation to white/intermediate soil (WI;  $F = 4.271$ ;  $p = 0.002$ ), and white/fine soil (WF;  $F = 1.584$ ;  $p = 0.088$ ). Plot names as in Figure 1. 4 defined clusters encircled. Different patterns on samples mark the 5 clusters found in a twinspan of the same data.

Table 4. F value, significance value and amount of variance ( $\lambda$ ) in the plant species data explained by the different environmental variables tested for the CA in Figure 2, as well as the total variation in dataset (total inertia). Acronyms as in Table 2.

Environmental variable	F	$\lambda$	p
WI	4.271	0.266	0.002
WF	1.584	0.097	0.088
Ds	1.557	0.093	0.112
GI + GF	0.761	0.046	0.638
Total inertia		2.157	

### *How does the variation in species composition between plots relate to differences in soil conditions and browsing intensity?*

The species composition was found to vary with the differences in soil type in the area (Figure 1–2, Table 4). However, I did not find as much variation in soil types as expected, i.e. no red and/or coarse sand was found in the surveyed plots (Table 5). To examine the relationship between the soil types present and woody vegetation distribution the plots are first divided in accordance to their species composition by the clusters found in the CA (Figure 2). 4 clusters of plots with similar plant species compositions can be identified:

**Cluster 1:** These plots are characterized by high abundances of acacias, particularly *Acacia hebeclada* that dominates in every plot. This vegetation is fairly open with scattered trees, and correlated with the soil type WF.

**Cluster 2:** Here we find *Lonchocarpus capassa* to be the most common species and the largest *Combretum hereroense* stands occur here as well. *A. hebeclada* and *C. mopane* are also found in low numbers. Plots in cluster 2 contain quite open vegetation with low tree densities.

**Cluster 3:** These plots are characterized by dense stands of *C. mopane*, sometimes making up as much as 90 % of all trees. *L. capassa* also occurs in most of the plots, and *Acacia erioloba*, *A. hebeclada*, *Boscia albitrunca* and *Lonchocarpus nelsii* are found in some. The woody vegetation in these plots is denser than in those of cluster 1 and 2 and correlates with soil type WI.

**Cluster 4:** In these plots we also find strongholds of *C. mopane* and occurrences of *L. nelsii*, *A. hebeclada*, *L. capassa*, *Dichrostachys cinerea* and *B. albitrunca*. The plots all have high densities of trees and correlates with soil type WI.

The TWINSpan confirmed cluster 1 and 2 except for two plots (MW200 and ME4000) that were not included in cluster number 2 and 4, respectively, contradicting the CA ordination (Figure 2). Clusters 3 and 4 were not separated in the same way from each other in the TWINSpan analysis as in the CA. TWINSpan further suggests the following main indicator species for the differences between clusters: *C. mopane*, *A. hebeclada* and *L. capassa*. A shared result for both methods of analysis is that all different clusters include plots both close and far from the water source.

Trends in browsing pressure across species (Table 6) can give us an overall idea of how general patterns of browsing manifest themselves. Ruminant, elephant and accumulated browsing are all positively correlated to each other. Both ruminant and accumulated browsing, but not elephant browsing, were negatively associated with the distance from the water source.



Table 5. Soil types in all plots (8 distances) along the four transects. Soil types by colour (W = white, G = grey, R = red) and texture (F = fine, I = intermediate, C = coarse)

Distance (m)	Marabou vlei		Rhino vlei	
	West	East	West	East
200	WF	GI	WI	WF
400	GF	GF	WF	GI
600	GF	WF	WF	GI
800	GF	WF	GI	GI
1000	WI	GI	GI	WI
2000	WI	WF	GI	WI
4000	WI	GF	WF	WI
5500	WI	GF	WF	WI

Table 6. Significant Spearman Rank Correlation coefficients ( $r_s$ ) of environmental factors, plant traits and browsing pressures across species. Acronyms as table 2.

Correlations across species			$r_s$	DF	p
R br	-	Acc br	0.45432	79	<0.0001
E br	-	Acc br	0.40709	79	<0.0001
R br	-	E br	0.35101	79	<0.0001
Acc br	-	Leaf size index	0.51612	79	<0.0001
R br	-	Leaf size index	0.35721	79	0.001
E br	-	Leaf size index	0.12804	79	0.002
R br	-	Ds	-0.36911	79	0.002
Acc br	-	Ds	-0.32182	79	0.006
Evergreenness	-	Ds	0.67296	9	0.030
Evergreenness	-	Acc br	-0.69157	9	0.038

*Can the variation in species composition between plots be explained by the plant herbivory-related strategies tolerance or resistance?*

When comparing the presence of individuals with specific traits in the 2004 and 2009 plots we find that some characteristics have become more common or rare (Table 7). Spinescence is a trait that has increased in occurrence while the traits N1, ADF2 and TP2 have been found to decrease. Evergreenness, TT1, TT2, ADF1, N2, and TP1 did not show a significant trend among plots (Table 7).

The abundance of evergreen individuals was positively correlated with distance from water source and negatively with accumulated browsing (Table 6). Moreover, the different browsing measures were also positively correlated with leaf size (Table 6).

Between plant characters and environmental factors/browsing pressures some relationships can be identified. Analysis indicates that accumulated browsing pressure was positively correlated with TP1, and soil type WF was negatively correlated with N1, TT2 and ADF2 in plant parts (Figure 3, Table 8) although none of these relationships have a correlation coefficient above 0.4. However, the chemical properties of N1, TT2 and ADF2 were all strongly correlated to each other (Table 8).

Table 7. Changes from 2004 to 2009 in abundance of individuals per plot displaying certain plant traits. T-values obtained from paired t-tests. Acronyms as in Table 2.

Trait	t-value	p	n
Spinescence	3.59	0.001	28
N1	-2.55	0.017	28
ADF2	-2.50	0.019	28
TP2	-2.29	0.030	28
TT2	-1.87	0.072	28
Evergreenness	-1.40	0.174	28
TT1	0.56	0.578	28
ADF1	-0.15	0.884	28
N2	0.12	0.907	28
TP1	-0.07	0.941	28

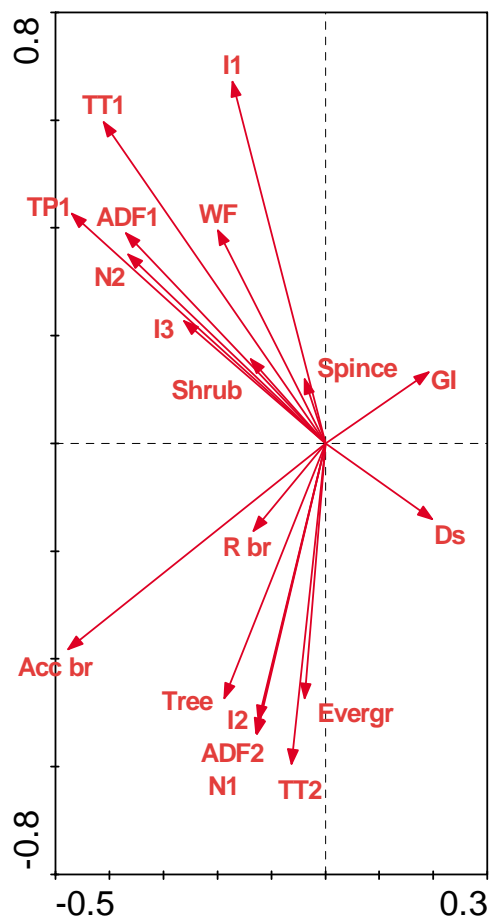


Figure 3. CCA ordination biplot showing relationships between herbivory-related traits, browsing pressures and environmental factors. Acronyms as in Table 2.

Table 8. Correlation coefficients for herbivory related traits and environmental factors calculated in the Canoco for Windows package for the CCA ordination illustrated in figure 3. Acronyms as in Table 2.

<b>Correlation coefficients between different herbivory related traits and environmental factors</b>																		
I2	-0.1594	1.0000																
I3	0.0521	-0.1969	1.0000															
Evergr	-0.0255	0.4898	-0.2156	1.0000														
Tree	-0.1000	0.9702	0.0148	0.4786	1.0000													
Shrub	0.3590	-0.1575	0.1876	-0.1212	-0.0484	1.0000												
Spince	0.4724	-0.0578	0.1433	-0.0706	0.0472	0.8505	1.0000											
TP1	0.4326	0.0665	0.5094	0.0645	0.1600	0.0797	-0.0650	1.0000										
TT1	0.3960	-0.2992	0.7721	-0.3010	-0.1142	0.2791	0.1099	0.7041	1.0000									
TT2	-0.2574	0.9844	-0.1649	0.4847	0.9655	-0.1666	-0.0341	-0.0517	-0.3433	1.0000								
N1	-0.2533	0.9456	0.0529	0.4364	0.9809	-0.0905	0.0043	0.0518	-0.1350	0.9700	1.0000							
N2	0.5995	0.2080	-0.1730	0.2343	0.1604	-0.0416	-0.1352	0.7030	0.2496	0.0393	-0.0078	1.0000						
ADF1	0.6127	0.1551	-0.1559	0.2142	0.1125	-0.0549	-0.1613	0.7205	0.2744	-0.0135	-0.0573	0.9922	1.0000					
ADF2	-0.2541	0.9462	0.0496	0.4357	0.9804	-0.0872	0.0092	0.0473	-0.1386	0.9706	0.9998	-0.0076	-0.0594	1.0000				
R br	-0.0203	0.1081	-0.0803	0.0926	0.1039	0.0268	0.1890	-0.0762	-0.1110	0.1294	0.1071	-0.0538	-0.0733	0.1098	1.0000			
Acc br	-0.2356	0.2474	0.3101	0.0668	0.2778	-0.2850	-0.2061	0.3073	0.0942	0.2518	0.2880	0.0184	0.0109	0.2867	0.3235	1.0000		
Ds	-0.0510	-0.1482	-0.1809	0.2190	-0.1895	-0.0700	-0.2110	-0.2296	-0.1817	-0.1591	-0.1965	0.0232	0.0246	-0.1949	-0.3640	-0.3973	1.0000	
GI	-0.2306	0.1197	0.3156	-0.2555	0.1770	0.0200	0.0117	0.1638	0.2407	0.1517	0.2396	-0.1728	-0.1813	0.2391	0.0637	-0.0608	-0.3296	1.0000
WF	0.3818	-0.2864	-0.0273	-0.2980	-0.2811	0.0736	0.2115	-0.0922	0.1072	-0.3016	-0.3175	0.0641	0.0684	-0.3155	0.0587	-0.0907	-0.0617	-0.3953
	I1	I2	I3	Evergr	Tree	Shrub	Spince	TP1	TT1	TT2	N1	N2	ADF1	ADF2	R br	Acc br	Ds	GI

*Is there an intraspecific variation in herbivory-related plant traits with distance to water?*

Finally I have addressed the question of intraspecific variation in herbivore associated traits. The only significant results were found in *L. nelsii* (Table 9). Leaf size is quite strongly positively correlated with both accumulated browsing and ruminant browsing which indicates that more severely browsed *L. nelsii* have larger leaves. Elephant browsing showed the same tendency to correlate with leaf size index although it was a weaker relationship and slightly above the significance level. No other correlation analyses yielded significant outcomes, but three analyses showed close-to-significant results. Two of them, concerning *A. hebeclada*, indicated that heavier browsing by ruminants results in larger leaflets whereas leaf size is negatively correlated with spine length in this species. The last close-to-significant result showed that *L. capassa* individuals which have been severely browsed in the past have smaller leaflets.

Table 9. Significant, and close-to-significant intraspecific Spearman Rank Correlation coefficients ( $r_s$ ) of plant traits related to herbivory and environmental factors. Acronyms as in Table 2.

<b>Intraspecific correlations</b>					
<b><i>A. hebeclada</i></b>			$r_s$	DF	p
R br	-	Leaflet size index	0.54752	9	0.0574
Leaf size index	-	Spine length	-0.53636	9	0.0892
<b><i>L. capassa</i></b>					
Acc br	-	Leaflet size index	-0.55021	11	0.0574
<b><i>L. nelsii</i></b>					
Acc br	-	Leaf size index	0.73786	8	0.025
R br	-	Leaf size index	0.717624	8	0.0272
E br	-	Leaf size index	0.406181	8	0.0836

## Discussion

Different patterns of vegetation densities have been found around artificial waterholes in earlier studies. In some cases, a sacrifice area and an increase of both shrub and tree densities with distance from the water is found (Brits *et al.* 2002, Chamaille-Jammes *et al.* 2009). It is explained by the typical pattern of animal densities creating the observed effect on the vegetation. Interestingly, there have also been studies revealing the opposite, that tree densities are increasing with time around waterholes and no conspicuous sacrifice area is present (Kalwij *et al.* 2010).

I have found that between the five years of surveys, vegetation compositions around the two artificial waterholes have changed and that areas closer than one km to the water source seem to have undergone more extensive changes in plant species composition than areas further away. My results also show that the different vegetation types in the area are not restricted to any particular location in relation to the water source (a result consistent with findings of *e.g.* Makhabu *et al.* 2002). Thus, all different types of vegetation are found within this highly disturbed area  $\leq 1$  km around the waterholes. I have found that one common plant species generally appears to be increasing in abundance while some others have been decreasing. It leads us to conclude that the vegetation around artificial waterholes does not change simply by a density decrease of all plant species present such as was proposed by Brits *et al.* (2002) but that the species compositions have changed as a result of some species doing better than others under different circumstances and that there may be some that are actually benefited by this manner of browsing. This has already been shown for herbaceous species, that those species residing close to artificial watering points are species adapted to this specific type of disturbances and those inhabiting areas further from the water are species adapted to more stable conditions and less grazing (Makhabu *et al.* 2002, Todd 2006).

I have shown that not all vegetation types have been changing equally much. For example I have found the same phenomenon as Chamaille-James *et al.* (2009) that dense stands of *Colophospermum mopane* are not much affected by intense browsing in terms of either species abundances or species compositions. This is a result of the tolerance ability of *C. mopane* and the creation of browsing lawns supporting intense browsing. Thus the degree of species composition change is dependant on the type of vegetation that is affected and likely caused by changed competitive patterns as a result of the herbivory related strategy used by different plant species occupying the spot. This may be of importance for future evaluations of old and planned new artificial waterholes since different vegetation communities and plant species are affected differently and consideration thereof must be taken. Also the composition of the animal community using the area may influence the response of woody species composition. More extensive studies of succession are needed in order to understand the underlying causes of these particular vegetation composition changes.

I found the assumption of a gradient with browsing pressure diminishing further from the waterhole to be generally true. Only elephants do not seem to be restricted in their feeding range by the 5.5 km radius around the watering points studied. This result is supported by Kasiringua's (2010) findings that herbivore densities (except elephants) were in fact diminishing with distance from these watering points, and is also consistent with general findings in this research field (*e.g.* Brits *et al.* 2002). The vegetation types were not restricted by the browsing gradient emanating from the waterholes as expected, but they were found on different types of soil. I therefore conclude that the artificial waterholes themselves, even after 20 years of existence, do not have a strong enough impact on the woody vegetation of the area to create the typical patterns described in some previous studies of other artificial waterholes. My result implies, in concordance with Chamaille-Jammes *et al.* (2009), that in this case soil characteristics are more important determinants of plant communities than water availability or browsing intensity.

Makhabu *et al.* (2002) found that grass species that were growing on sandy soils were effectively restricted by the proximity to the water source while grasses growing on calcareous soils were not. If this is also true for woody vegetation it could explain why I did not see the expected vegetation gradients with changing species compositions out from the waterholes simply because there were mostly alluvial soils in the plots. Since I did not find the whole scale of soil types as expected, ranging from Kalahari sand to alluvial clay, and since the two soil types with significant effects are quite ecologically similar in terms of nutrient content and water holding ability, I was not able to satisfactorily evaluate the importance of soil properties, soil nutrients and water availability for the distribution of vegetation types in the area.

Soil type may also be of some importance for how the vegetation changes in the species composition with time. One of the soil types (WI) showed correlation to plots that in general have not changed much. This indicates that soil characteristics, such as nutritional contents and ability to hold water is important for the stability of the vegetation composition and that differences in soil types will have significant effects on the permanence of the residing vegetation. Perhaps soil conditions could be further used as indicators when evaluating places for additional watering points where and if responsible authorities decide them necessary. If nutritional contents of the soil indeed is linked to the prevailing herbivore defence strategy and assuming that there is adequate knowledge about local species response to herbivory, then knowing the geology of an area may give an indication of the type of plant species and plant communities that will be able to sustain conditions around watering points in semi-arid zones. This could perhaps further explain why there have been such different previous results of woody vegetation density patterns around such waterholes.

Evergreen plants, typical representatives of the resistance strategy, were found growing far from the water where herbivore densities are lowest and in other places where the browsing intensity was light. During the dry season when most plants have shed their leaves, evergreen plants are fully exposed to herbivores. Whereas deciduous plants often store resources in stems, roots or in special storage tissues, evergreens do not withdraw resources from photosynthetic tissues and many do not have special storage organs (Skarpe & Hester 2008). Therefore they are especially vulnerable to the intense browsing of the dry season which is avoided by deciduous, both resistant and tolerant, species. Heavy defences are thus essential to protecting resources and securing next years growth (Skarpe & Hester 2008). It is not surprising then that these types of plants have greater difficulties sustaining the environment close to these permanent water sources.

There was also a second result concerning chemical traits, signaling plants employing resistance strategy as not so successful close to water points. Typical chemical defences such as high phenol, high fiber concentration and low content of nitrogen in plant parts seem to be unfavourable in this environment. Plant species showing these characteristics are declining around Rhino and Marabou vlei, thus posing the question if tolerant species are coping better. This study has not been able to sufficiently prove or refute this proposition.

High concentrations of chemical defence compounds are often coupled with high fiber and low nitrogen content in plant parts, which is a way for plants to resist herbivory since it render tissues low in nutrition and difficult to digest for herbivores. These relationships were confirmed in my analysis. The mentioned chemical properties were also negatively related to the soil type WF which indicates that this type of resistance to herbivory is not found in places with alluvial fine clay. Plants primarily relying on the resistance strategy for avoiding browsing are the ones that are adapted to nutrient poor soil conditions according to the theory of herbivory related strategies (Coley *et al.* 1985). My results agree with this theory since the nutritious alluvial soils of the former Savuti lake would favour the fast growing tolerant species as opposed to the slow growing resistant species.

That I did not see any more distinct relationships between soil types and the herbivory related strategies may be explained by the lack of variation in soil types. Perhaps the expected patterns were not more visible simply because I did not find as much variation in soil conditions as expected. The theory of soil nutritional states being the major factor deciding the most efficient strategy by which plants should respond to herbivory clearly states that differences in soil types are tightly connected to differences in strategies (Coley *et al.* 1985). If this is true then I would not find enough variation in strategies here for a pattern to be visible.

I did not find any indication of defence strategies varying with the distance to water, but there was one indication of plant functional traits varying with browsing intensity as there was a positive correlation between low phenol concentrations and accumulated browsing. It signals that browsing is more intense where plants tend to have little chemical defence substances in tissues. This pattern could be a result of established browsing lawns for example, where tolerant plants with palatable leaves resprout to support more intense browsing, and browsing in return induces more resprouting in the tolerant plants.

Within species I found functional traits induced by herbivory in two common plant species, *Lonchocarpus nelsii* and *Acacia hebeclada*. In *L. nelsii* I found larger leaves on plants that had been severely browsed than on plants that had not been browsed. This is thus a clear example of a species employing the tolerance strategy. One benefit of having large leaves is that large leaves often have a large specific leaf area (area per weight unit). This is believed to involve a potentially high photosynthetic rate which is essential in order to rapidly replace lost tissue (Skarpe & Hester 2008). This would explain the benefit of tolerance in this species.

I found a tendency in the spiny *A. hebeclada* to have larger leaflets when browsed by ruminants. This cannot be explained by the theory of bite sizes. Spines function as defence against twig biting and leaf stripping by dividing the shoot and reducing the possible bite size of the herbivore (Cooper & Owen-Smith 1986, Wilson & Kerley 2003). It thus offers a smaller intake rate than a nonspinescent species with similar sized leaves (Cooper & Owen-Smith 1986). Increasing leaflet size after being browsed would not give *A. hebeclada* any advantages in terms of bite size defence. Another benefit must come into play to counterbalance the cost of this increased regrowth. Most probably this is achieved by the higher photosynthetic rate possible with more green tissue.

*A. hebeclada* is anyhow showing both anti-herbivore strategies, resistance in form of spines and tolerance in the regrowth of larger leaflets. But since I also found that plants of this species with larger leaves tend to have shorter spines, there may be a trade-off between the two strategies in this case. A more specific study will be necessary to verify this hypothesis. Whatever benefit given by their compensatory regrowth it seems to be working at least for *A. hebeclada* since this species is seemingly increasing in the area.

Contradictory to hypothesis, *Lonchocarpus capassa* showed a tendency to have smaller leaflets when severely browsed. This may be an effect of resource allocation. Some species may respond to herbivory by increasing shoot numbers and as a result of energy limitations reduce the size of the new shoots and/or leaves (Skarpe & Hester 2008). This would create the pattern seen in *L. capassa*. I did not have the opportunity to study changes in shoot densities before and after browsing. A separate study of this species is thus needed in order to confirm this hypothesis.

In conclusion I want to stress the point that many of the previous studies done on vegetation around artificial waterholes have been concerned with studying vegetation composition in relation to distance from the water and browsing intensity. This study emphasizes the importance of soil properties and plant responses to herbivory on the change and structure around artificial watering points in southern African ecosystems.

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