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ARTICLE

EFFECTS OF FENCING ON FORAGE BIOMASS AND QUALITY THROUGH LIVESTOCK EXCLUSION FROM A PROTECTED AREA IN THE SOUTHERN KALAHARI

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Abstract. The substitution of wild herbivores by livestock has led to substantial degradation of many southern African grazing systems. As a result, bush and shrub encroachment has led to a reduction of grasslands, invasion of thorn shrubs, reduced carrying capacity of range land, and desertification. These changes often raise socio-economic challenges for rural communities in arid and semi-arid regions, as previously profitable areas may become no longer economically viable. This study aims to compare biomass and key chemical characteristics of grassy vegetation between sites experiencing low vs. high grazing pressures. Furthermore, we estimate the recovery time needed for pasture in heavily grazed areas to reach properties of similar sites under low grazing pressure. In heavily grazed areas, grass was of higher quality than in areas with low grazing pressure, as the remaining or re-growing grass contains higher percentages of protein and lower concentrations of fiber. However, as heavy grazing led to reduced grass biomass, the absolute amount of protein available per unit area was lower in areas with high compared to areas with low grazing pressure. Furthermore, at the heavily grazed area we recorded a high proportion of unpalatable plant species. The exclusion of livestock through fencing resulted in a rapid increase of grass biomass and therefore higher amounts of fibre, protein and hemicellulose contents per unit area after one wet season, whereas the chemical concentrations of plant compounds changed remarkably little after elimination of livestock grazing pressure.

In areas where cattle substitute wild-ranging herbivores we recommend livestock managers consider transitioning to sustainable grazing systems through grazing rotation, diversification of herbivore species, and reduction in stocking rates. This would secure sustainable livestock-based livelihoods while avoiding permanent rangeland degradation due to bush encroachment and desertification.

Keywords: fencing, grass recovery, grass biomass, plant chemistry, bush encroachment, desertification, livestock, heavy grazing

INTRODUCTION

Fifty percent of the world's terrestrial surface area is covered by rangeland, large parts of which support wild-ranging herbivores (Gordon 2006). Different herbivore species are supported by different habitat types with varying plant communities, mainly driven by abiotic factors such as soil characteristics and climate. Hobbs (1996) described three feedback loops from herbivores to plant communities: the regulation of process rates, the modification of spatial mosaics, and the possible control of transition between alternative ecosystem states. Herbivores influence plants in various ways and at different scales, reaching from the direct impact through feeding damage to alteration of plant communities due to selective feeding behaviour (Benthien *et al*. 2018, Borer *et al*. 2014, Milchunas & Lauenroth 1993, Stolter *et al*. 2018 a and b). The magnitude of the impact of herbivores on plant systems depends on a variety of factors such as intensity and timing of grazing or browsing, herbivore species composition, competition between herbivore or plant species, as well as abiotic factors such as climate.

Feeding damage can lead to changes in the chemical composition of plants with wide-reaching consequences. While some plant species respond to grazing or browsing pressure by producing feeding deterrents, others simply compensate losses in biomass by increased growth of high-quality parts (Fornara & du Toit 2007, Schönbach *et al*. 2011, Stolter *et al*. 2005). Changes in the chemical composition of plants due to feeding damage can lead to changes in their utilization by subsequent herbivores (Danell & Huss-Danell 1985, Herder *et al*. 2009, Stolter *et al*. 2008 a and b), while the composition of plant primary compounds (e.g. nitrogen) as a nutritional source for herbivores, and plant secondary compounds (e.g. tannins) as defence mechanisms against browsing, might affect the attractiveness of plants to utilization by herbivores. The impact of herbivores on plants, therefore, can lead to cascading responses throughout different trophic levels, from the soil microbial community (Qu *et al*. 2016, Teague *et al*. 2011, Turchin *et al*. 2000, van der Wal *et al*. 2004) to herbivore communities serving as a prey base for apex predators (Krebs *et al*. 1995, Turchin *et al*. 2000).

Historically, African grazing systems are shaped by the seasonal movements of wild wide-ranging large herbivores. However, due to changes in land-use patterns, large areas are now grazed continuously by cattle. High levels of livestock grazing are known to cause high losses of green leaf biomass, annual net primary production, grass coverage (Boone 2005, Perkins 1996, Verlinden *et al*. 1998, Zeng *et al*. 2017), and changes in ecosystem processes, which lead to bush encroachment and the decline in palatable species (Boone 2005, Joubert *et al*. 2008, Noy-Meir 1982, Walker & Noy-Meir 1982, Walter 1954). Although bush encroachment is assumed to be a natural process in savannah succession (Ward 2005), it is exacerbated through heavy grazing pressure from livestock in combination with a decline in browsers, fire suppression and climatic effects (Joubert *et al*. 2008, Moleele *et al*. 2002, Skarpe 1990). In southern Africa, bush or shrub encroachment is caused mainly by different *Acacia* species and represents a major challenge as it leads to reduction of grasslands, invasion of inedible thorn shrubs and thus to reduced carrying capacity for grazing herbivores. Together with some other plant species, such as *Dichrostachys cinerea*, *Euclea undulata*, *Grewia flava* and *Lycium namaquense* (Moleele & Perkins 1998, Skarpe 1990), bush encroachment causes socio-economic problems in arid and semi-arid regions as previously profitable areas may become no longer economically viable (Smit 2004). Especially in arid regions, high grazing pressure may further fuel the loss of soil fertility through erosion and drive desertification of formerly productive grassland (Schlesinger *et al*. 1990).

The Kalahari Transect Wet Season Campaign documented increased grazing pressure in the southern Kalahari, bordering and affecting Botswana's Khutse Game Reserve (KGR) and the southern border of the Central Kalahari Game Reserve (CKGR), where cattle replaced migratory wildlife (Shugart *et al*. 2004). In 2009, a game fence was installed along the borders of KGR and CKGR, in order to protect livestock from predation by African lions (*Panthera leo*). Before fence construction, livestock heavily grazed the eastern border of KGR and the southeastern border of CKGR. The exclusion of livestock from the game reserves after fencing provided an opportunity to study the effects of livestock grazing on grass biomass production and its chemical composition. It further allowed us to monitor changes under different grazing regimes over time, and to provide insights into the impacts of fencing on the delivery of food provisioning services (Durant *et al*. 2015). Adapting this situation for an experimental approach we addressed the following questions:

1. How does standing biomass of grassy vegetation and key chemical characteristics differ between sites with low and high grazing pressure?
2. Where differences are detected, how long does it take for pasture in heavily grazed areas to recover from heavy grazing sufficiently to approach the properties of pasture under low grazing pressure?

MATERIALS AND METHODS

Study site

The study was carried out along the eastern boundary of Khutse Game Reserve (KGR), Botswana. The KGR (2 600 km2) is situated between 23°-24° S and 24-25° E, within the Kweneng District in the southern part of the country, bordering the Central Kalahari Game Reserve (CKGR, 52 000 km2) in the north. The semi-arid climate is characterized by a cold dry season (April-September) and a hot wet season (October-March), annual rainfall averages 300 mm (de Vries *et al*. 2000) and average monthly temperatures range between 8.5-35.5°C (Thomas & Shaw 1991). The landscape is predominantly flat and characterized by tall grass, thorn bush thickets with scattered acacia trees, and open salt pans. In October 2009, an electrified double game fence (2.7 m high wire netting fence with four electrified wires; 1.5 m high wire netting cattle fence) was completed along the southern and eastern border of KGR and the southeastern corner of CKGR, resulting in a barrier of about 300 km, aiming to mitigate livestock predation by lions. More details on the fence and its effects on native wildlife are provided in Kesch *et al*. (2014).

Three sampling sites were installed in three different areas: Site 1 (23°21'54" S, 24°37'24" E) was located just outside the protected area and characterized by intensive livestock grazing, mainly cattle. Site 2 (23°21'48" S, 24°37'16" E) was located just inside the fenced reserve and was subject to a comparable livestock grazing pressure as Site 1 before fencing. Due to the exclusion of livestock in October 2009, grazing pressure was reduced to a comparable intensity as Site 3. Site 3 (23°20'33" S, 24°32'55" E) was located 8 km inside KGR and characterized by low grazing pressure by wildlife such as gemsbok (*Oryx gazella*) and red hartebeest (*Alcelaphus buselaphus*).

At each site, a grid of 21 sampling plots (each sampling plot 10 x 10 cm^2) was established, spaced at regular intersite distances of 20 m. Plots were sampled in June 2009 (dry season), September 2009 (dry-wet), December 2009 (wet), March 2010 (wet-dry) and June 2010 (dry 2). During each sampling month, all grass material in each of the 21 sampling plots per site was cut 5 cm above the ground. In order to avoid sampling the same plots again, transects were shifted north by 1 m every three months. Grass biomass was measured as wet weight immediately after cutting and as dry mass after drying in the sun until sample weights had reached a plateau.

Chemical analyses

Plant material harvested from each 10 x 10 cm^2 sample plot was pooled and chemical analyses were run separately for each plot if enough plant material was available. Acid Detergent Fiber (ADF) and Neutral Detergent Fiber (NDF) present components of the cell wall. ADF consists of cellulose, lignin and minerals. Cellulose is digested by symbionts in the rumen and delivers the main energy for ruminants, whereas lignin is indigestible for most ruminants. NDF consists of ADF plus hemicellulose, which is digestible by all herbivores. Hemicellulose (HC) amounts are calculated by subtracting ADF from NDF. Nitrogen in grass is mostly contained within proteins and can be converted to crude protein by multiplication by the standard factor of 6.25 (Robbins 1983). Analyses of these components were carried out at the chemical laboratory of the Department of Animal Ecology and Conservation at the University of Hamburg in Germany and followed procedures described by Stolter *et al*. (2005). Where plant material collected was insufficient for chemical analyses, two to three samples were combined per site and date.

The amount of protein and hemicellulose per unit area was calculated by multiplying the dry biomass per 100 cm^2 sample with the average concentrations of protein and hemicellulose for the plot and date.

Statistics

Because the amounts of protein and hemicellulose per unit area as measurements of dry biomass deviated from normality, we applied non-parametric Kruskal Wallis Analysis of Variance (X^2) to the analyses of biomass production. For the different sites and sampling times, the concentrations of NDF, ADF, hemicellulose and crude protein did not deviate from normality. Accordingly, for the concentrations of these chemical components we applied a parametric ANOVA with *post-hoc* tests, using the software IBM SPSS 22.0.

RESULTS

Biomass

Biomass per unit area of Site 1 (high grazing pressure from livestock) was always significantly lower than at Site 3 (low grazing by wildlife) (Table 1). Site 2 (livestock excluded after October 2009, before the onset of the wet season) did not differ from Site 1 before fencing but differed significantly from Site 3. After construction of the fence and the onset of the wet season, biomass at Site 2 increased compared to Site 1. The difference in biomass between Sites 1 and 2 became significant only after the wet season in June 2010 (measurement in the subsequent dry season), when biomass at Site 2 was statistically no longer different from biomass at Site 3. The standing biomass of grass remained stable at Sites 1 and 3 throughout the year.

Fiber

For most of the year, fiber content varied among sites (Table 1). At the transition between dry and wet seasons ('dry-wet'), there was a tendency for a lower content of all fiber fractions at Site 1. In December ('wet'), at the beginning of the wet season, fiber concentrations were significantly lower at Site 1 than at the other sites.

Crude Protein

Crude protein concentrations were always significantly higher at the site with heavy livestock grazing pressure (Site 1) than at Site 3. Site 2 resembled Site 3 throughout the study period in terms of crude protein concentration.

Absolute nutrient availability

In absolute terms, the amount of protein and hemicellulose available in plant biomass per unit area was always highest at Site 3 and remained high at this site year-round. Before fencing, nutrient availability at Site 2 resembled that at Site 1 but shifted towards Site 3 after installation of the fence (Table 1).

Differences within grass species between sites

In June 2010 ('dry 2'), species were identified at plots that harbored only a single grass species. Due to the restricted sample size the comparison of different chemical components was only feasible for spear grass (*Heteropogon contortus*) (Table 2). The results for spear grass from different sampling sites matched the results for samples with pooled species, where acid detergent fiber was lowest and protein was highest at Site 1 which had the highest grazing pressure (Table 2).

Table 1. Grass biomass (dry weight) and chemical composition under three different regimes of grazing pressure. Values for biomass, protein and hemicellulose (HC) per 100 cm^2 are medians and quartiles based on dry mass of plants in grams cut in twenty-one 100 cm^2 plots per site and month. Values for chemical components are means ± standard deviation (in % of dry mass); N = sample size for the samples available for chemical analyses. Values for hemicellulose and protein per 100 cm^2 were calculated as the median biomass times the mean concentration of HC or protein, respectively. Statistics are based on Kruskal-Wallis-Analysis of Variance for biomass, protein and HC per 100 cm^2 (X^2-values) and ANOVA for chemical items (F-values). Different superscripts indicate different median/ mean values according to post-hoc tests. Significance levels are marked with asterisks: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Item	Season / year	Site 1 Livestock present	Site 2 Livestock excluded after October 2009	Site 3 No livestock	Statistics
Grazing pressure		high	high	low	
Biomass [g / 100cm^2]	Dry / 2009	3 – 4^{a} – 8	5 – 10^{a} - 23	10 – 25^{b} – 96	X^2 = 22.62***
	Dry-wet / 2009	0 – 2^{a} – 8	0 – 2^{a} – 8	4 – 24^{b} – 33	X^2 = 13.43***
	Wet / 2009	0 – 3^{a} – 8	0 – 13^{a} – 28	9 – 31^{b} - 51	X^2 = 16.72***
	Wet-dry /2010	0 – 3^{a} – 8	7 – 15^{a} - 29	12 – 26^{b} - 60	X^2 = 16.51***
	Dry / 2010	0 – 2^{a} – 6	15 – 24^{b} – 46	29 – 33^{b} - 71	X^2 = 26.88***
NDF [%]	Dry / 2009	68.3 ± 7.2	71.7 ± 4.1	72.2 ± 3.4	F = 2.61
	Dry-wet / 2009	64.8^{a} ± 6.6	72.7^{b} ± 3.5	71.5^{ab} ± 3.7	F = 7.54**
	Wet / 2009	57.8^{a} ± 14.8	71.8^{b} ± 6.5	76.0^{b} ± 4.7	F = 13.99***
	Wet-dry /2010	70.1^{a} ± 10.9	77.4^{b} ± 4.3	77.1^{ab} ± 3.8	F = 5.80**
	Dry / 2010	71.0 ± 11.1	76.3 ± 4.0	73.7 ± 4.8	F = 2.56
ADF [%]	Dry / 2009	45.2 ± 5.1	44.8 ± 6.0	42.1 ± 4.3	F = 1.67
	Dry-wet / 2009	39.9 ± 2.7	42.3 ± 4.9	42.3 ± 3.6	F = 1.22
	Wet / 2009	35.1^{a} ± 5.6	43.2^{b} ± 4.8	46.1^{b} ± 4.8	F = 15.31***
	Wet-dry /2010	43.0^{a} ± 5.4	42.9^{a} ± 3.2	47.2^{b} ± 4.6	F = 5.64**
	Dry / 2010	44.6 ± 6.3	43.1 ± 2.8	43.3 ± 5.0	F = 0.32
HC [%]	Dry / 2009	23.1^{a} ± 7.5	26.9^{ab} ± 6.8	30.1^{b} ± 1.6	F = 5.42**
	Dry-wet / 2009	24.9^{a} ± 7.0	30.3^{b} ± 2.6	29.2^{ab} ± 2.5	F = 4.23*
	Wet / 2009	22.6^{a} ± 10.4	28.5^{ab} ± 6.4	29.8^{b} ± 2.1	F = 4.13*
	Wet-dry /2010	27.0^{a} ± 7.8	34.4^{b} ± 2.6	29.9^{a} ± 3.8	F = 10.28***
	Dry / 2010	26.4^{a} ± 11.7	33.2^{b} ± 3.1	30.4^{ab} ± 2.3	F = 5.13**
Protein [%]	Dry / 2009	6.0^{a} ± 2.6	4.7^{ab} ± 1.9	3.5^{b} ± 0.6	F = 7.25**
	Dry-wet / 2009	6.3^{a} ± 3.2	3.9^{b} ± 1.8	3.2^{b} ± 0.5	F = 8.68***
	Wet / 2009	9.9^{a} ± 3.8	5.4^{b} ± 2.7	4.6^{b} ± 3.3	F = 9.11***
	Wet-dry /2010	7.2^{a} ± 3.2	4.8^{b} ± 0.9	4.2^{b} ± 1.1	F = 11.51***
	Dry / 2010	6.7^{a} ± 3.1	3.7^{b} ± 1.1	3.7^{b} ± 0.7	F = 13.27***
Protein [g / 100cm^2]	Dry / 2009	0.1–0.2^{a} –0.5	0.2-0.5^{a} -1.1	0.4-0.9^{b} -3.3	X^2 = 13.03***
	Dry-wet / 2009	0–0.1^{a} -0.5	0-0.1^{a} -0.3	0.1-0.8^{b} -1.1	X^2 = 10.29**
	Wet / 2009	0-0.3^{a} -0.7	0-0.7^{ab} -1.5	0.4-1.4^{b} -2.3	X^2 = 9.19**
	Wet-dry /2010	0-0.2^{a} -0.6	0.3-0.7^{ab} -1.4	0.5-1.1^{b} -2.5	X^2 = 10.94**
	Dry / 2010	0-0.1^{a} -0.4	0.5-0.9-1.7	1.1-1.2^{b} -2.6	X^2 = 21.28***
HC [g / 100cm^2]	Dry / 2009	0.7-0.9^{a} -1.8	1.2-2.7^{b} -6.2	3.0-7.5^{b} -28.7	X^2 = 26.64***
	Dry-wet / 2009	0-0.5^{a} -2.0	0-0.6^{a} -2.3	1.2-7.2^{b} -9.6	X^2 = 13.46***
	Wet / 2009	0-0.7^{a} -1.7	0.1-3.7^{b} -7.9	2.5-9.2^{b} -15.2	X^2 = 18.84***
	Wet-dry /2010	0-0.8^{a} -2.2	2.2-5.2^{b} -9.8	3.6-7.8^{b} -17.8	X^2 = 17.66***
	Dry / 2010	0-0.5^{a} -1.6	4.8-8.0^{b} -15.1	8.8-10.0^{b} -21.6	X^2 = 28.23***
Sample size	Dry / 2009	N = 14	N = 16	N = 16	
	Dry-wet / 2009	N = 8	N = 8	N = 17	
	Wet / 2009	N = 10	N = 13	N = 17	
	Wet-dry /2010	N = 11	N = 20	N = 19	
	Dry / 2010	N = 8	N = 21	N = 21	

NDF = Neutral detergent fiber; ADF = Acid detergent fiber; HC = hemicellulose

Table 2. Chemical composition of Spear grass *H. contortus* collected in June 2010 (dry 2) at sites of different grazing pressure. N = sample size; significance levels are marked with asterisks: * p < 0.05, ** p < 0.01, *** p < 0.001.

Chemical compound	Site 1 Livestock present	Site 2 Livestock excluded after October 2009	Site 3 No livestock	F (differences between sites)
Grazing pressure	high	Low	low	
N	3	2	11	
NDF [%]	76.0 ± 3.7	71.6 ± 42.1	76.9 ± 2.5	2.28
ADF [%]	42.3 ± 1.5	42.1 ± 1.5	47.0 ± 3.0	4.65*
HC [%]	33.7 ± 3.3	29.5 ± 3.5	30.0 ± 2.1	2.98
Protein [%]	6.1 a ± 0.6	4.6 ab ± 0.1	3.5 b ± 0.9	13.13***

Differences between grass species per site

The comparison of the chemical composition among grass species within a given site was restricted to species for which we obtained more than one sample in June 2010 ('dry 2'). This limited opportunities for comparison among grass species with Site 2 (*H. contortus*, *Pogonarthia squarrosa*, *Eragrostis contortus* and *Anthephora pubescens*). Protein concentrations differed significantly among the species. All other nutritional components showed no significant differences (Table 3).

Table 3. Chemical composition (in %) of different grass species collected in June 2010 (dry2) at site 2 (livestock excluded after October 2009) of low grazing pressure. N = sample size; significance levels are marked with asterisks: * p < 0.05, ** p < 0.01, *** p < 0.001.

Chemical compound	Spear grass (Heteropogon contortus	Herringbone grass (Pogonarthria squarrosa)	Lehmann's love grass (Eragrostis contortus)	Wool grass (Anthephora pubescens)	F (differences between sites)
N	2	2	12	3	
NDF [%]	71.6 ± 42.1	77.8 ± 2.1	78.2 ± 2.9	74.2 ± 3.6	2.85
ADF [%]	42.1 ± 1.5	46.2 ± 1.0	43.5 ± 2.6	42.8 ± 2.3	0.42
HC [%]	29.5 ± 3.5	31.7 ± 1.1	34.6 ± 2.2	31.3 ± 5.1	2.88
Protein [%]	4.6 ab ± 0.1	3.4 a ± 0.7	3.1 a ± 0.5	5.7 b ± 1.5	11.92***

DISCUSSION

This study aimed to describe differences in standing biomass and selected key chemical characteristics of grassy vegetation under low and high grazing pressure. Over the annual cycle, plants from the heavily grazed area always contained higher concentrations of protein (measured as nitrogen) than plants from areas of low grazing pressure, which is particularly clear in the intra-species comparison of *H. contortus* growing at all three sites. This can be explained by the consumption of most of the standing biomass in heavily grazed areas, as evidenced by an overall lower biomass compared with that observed at sites subject to lower grazing pressure. In the dry season, standing grass biomass is dominated by moribund plant material with low protein content, which is removed by heavy grazing. This results in a higher proportion of protein in new growth compensating for high grazing pressure in what little standing biomass remains (Biondini *et al*. 1998, Georgiadis & McNaughton 1990, Stolter *et al*. 2018b). At the beginning of the wet season in December, low fiber content at Site 1 reflects the high proportion of new growth and the lower proportion of old grass due to heavy grazing by livestock year-round. At Site 3 (no livestock), however, the relatively lower quality (based on protein content) of fodder in the area of low grazing pressure is compensated by the high biomass available. As a result, the total amount of protein available per unit area is much higher in the area of low grazing pressure than in the area of high grazing pressure.

Apart from the "left-over hypothesis" described above that is linked to a higher percentage of moribund grass at sites with low grazing activity, another reason for the higher concentration of nitrogen, and therefore protein, on heavily grazed sites might be the fertilization by dung and urine of herbivores (Barthelemy *et al*. 2018, Hobbs 1996, McNaughton *et al*. 1997). The area heavily grazed by livestock will be subject to high rates of cattle defaecation providing a potential source of nitrogen that is rapidly available to plants. Varying textures of different herbivores' faeces determine decomposition time and, in contrast to cattle dung, antelope faeces are known to take several months to degrade and, accordingly, for nutrients to become available to plants (Uunona 2015).

Nitrogen concentrations in plants may further be directly connected to nutrient cycling below-ground. Holland & Detling (1990) and Hamilton & Frank (2001) found that grazed plants decreased root carbon inputs into the soil via the rhizosphere, resulting in lower carbon availability to decomposers and a subsequent increase in plant-available nitrogen. This might be an explanation for the ability of plants to respond to grazing with higher nitrogen contents, which is often related to compensatory growth, as shown for other grass species (Fanselow *et al*. 2011) and woody plants such as *Dichrostachys cinerea* (Stolter *et al*. 2018b) and *Acacia nigricans* (Fornara & du Toit 2007). Additionally, at the heavily grazed site, a species of Fabaceae, *Elephantorrhiza elephantina*, was abundant and this plant family is known for its ability to fix nitrogen and thus improve soil quality. We conclude that the higher nitrogen content in plants growing under high grazing pressure may not only be due to a relatively high proportion of new growth in overall plant biomass.

Another reason for the differences among sites may be due to differences in plant species composition. The same plant species differed in its chemical composition across sites and different plant species could have different chemical properties even when growing at the same site (e.g. *H. contortus*). In order to account for selective as well as non-selective grazers in this study we collected "fodder" per unit area without discriminating among plant species and parts. We cannot identify, therefore, whether the chemical differences among sites were caused by consumers, by different plant species composition or by different chemical characteristics of the same plants growing under different grazing regimes.

Furthermore, higher nitrogen concentration in leaves might influence the nutrient turnover positively by enhancing the quality of litter which, in turn, might decompose more readily. In heavily grazed areas (e.g. Site 1 and Site 2 before fencing), this type of litter is very limited, and the impact of grazing on soil fertility might depend predominantly on the grazing history of the area. It is important to note however that unspecific site effects such as precipitation-dependent litter decomposition rates or fire have the potential to override all other factors contributing to nitrogen availability to plants (McNaughton 1985, Powers *et al*. 2009). For this study though, these effects are assumed to be limited as the study sites did not burn during the study period, and the study period further did not provide sufficient time for nitrogen in grassy litter to become available in soil through decomposition after the exclusion of heavy grazing at Site 2.

During the study, we further assessed how much time would be needed to restore pasture in heavily grazed areas by evaluating convergence in their chemical properties with levels in pasture under low grazing pressure. Our results showed that grass biomass in a formerly heavily grazed area in the Kalahari needed one wet season to recover from heavy grazing. Biomass production at sampling Site 2 (just inside the fence) increased dramatically with the beginning of the wet season. Already in December 2009 (wet), there was no longer a significant difference between the formerly heavily grazed area and the low grazing area inside the reserve. By the end of the wet season in March 2010 ('wet-dry'), the biomass at Site 1 (high grazing by livestock) started to be significantly different from biomass at Site 2 (fenced for about nine months). At first glance these results sound encouraging but we must keep in mind that these only refer to grass biomass.

Based on qualitative assessments, plant species composition within Site 2 did not change during the study period. Species composition remained very different from the low grazing control area inside the reserve. *Heteropogon contortus* (Spear grass) dominated the species composition in the low grazing area. *Eragrostis lehmanniana* (Lehmann's love grass) represented the main species in the formerly heavily grazed area. Lehmann's love grass is known to grow in areas with past disturbances (van Oudtshoorn 1999) and is therefore an indicator for formerly heavily grazed areas, as confirmed in this study. It is a valuable fodder grass in arid regions and often re-sowed on sandy or loamy soils in arid regions (van Oudtshoorn 1999). In contrast, Spear grass is one of the most common grasses in southern Africa. It is only palatable in early summer, can grow on poor soils, and is very resistant to fire (van Oudtwhoorn 1999). Other studies found an increase in abundance of unpalatable plants (Diáz *et al*. 2007) or of plants with high grazing tolerance (Todd & Hoffman 1999) in response to grazing pressure. This was also obvious at Site 1, where *E. elephantina* was the dominant deciduous scrub and seems to be avoided by cattle. *Elephantorrhiza elephantina* is known to become abundant at heavily grazed sites (van der Walt & le Riche 1999) and parts of this medicinal plant are being used as an enema for dysentery and diarrhoea, to treat mange and relieve constipation (Msimanga *et al*. 2013). This dominance might indicate the importance of combining grazers and browsers for efficient pasture utilization and avoiding under-utilization or fostering the high abundance of specific plants.

Milchunas & Lauenroth (1993) found that changes in dominant species are most evident during the early years of comparisons between grazed and ungrazed areas. Changes in plant composition, however, seem to be more sensitive to changes in ecosystem-environmental independent variables than to changes in grazing variables (Biondini *et al*. 1998, Milchunas & Lauenroth 1993, but see Fanselow *et al*. 2011). Furthermore, timing of grazing (Bullock *et al*. 2001), grazing history (e.g. duration and intensity, Tessema *et al*. 2011) and herbivore species composition (Allred *et al*. 2012) seem to be important determinants for changes in plant community structure. Since our work was a short-term study, we focused mainly on short-term changes such as plant-chemistry and biomass. Further investigations of the long-term changes in plant community structure would be beneficial to improve further our understanding of grazer-plant interactions in this area.

The results of our study show that grazing leads to higher protein content in continuously grazed areas. This result might reflect the possibility of the plant to respond to grazing (grazing tolerance) and its ability to access essential nutrients. Heavy grazing had a negative influence on biomass production in grasses, simply because all grasses were consumed by cattle. The exclusion of livestock resulted in a rapid increase of biomass even after years of heavy grazing, which demonstrates the potential of these plants to recover from grazing quickly, though changes in plant species composition were not evident one year after exclusion of livestock grazing. Within the relatively short time frame of our study, changes in plant species composition were not to be expected after the installation of the fence. It is important to note, though, that there were marked differences among sites exposed to different long-term grazing regimes, with an increased abundance of unpalatable plant species at the heavily grazed site. In anthropogenic grazing systems, where cattle substitute wild-ranging herbivores, natural long-distance movements are no longer possible. The avoidance of pasture degradation, including long-term negative impacts such as changes in plant species composition, increases bush encroachment or desertification that lead to a reduction in livestock-based livelihoods, requires a sustainable rangeland management strategy. Such a strategy should minimise pasture degradation and change by reducing stocking rates, making use of rotating grazing systems, and diversifying herbivore species by including wildlife together with livestock. These techniques can help to maximise rangeland production systems to deliver sustainable livelihoods while fostering wild herbivores and ensuring sustainable rangeland development (e.g. Dickhoefer *et al*. 2010, Fynn *et al*. 2016).

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