



Role of Herbivore Impact and Subsequent Timing and Extent of Recovery Periods in Rangelands☆☆☆



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ABSTRACT

The productivity and stability of cattle production on rangelands depends on the maintenance of a dense and productive perennial grass – dominated resource base, which is contingent on appropriate grazing and recovery periods. We investigated the effect of simulated trampling, dung inputs, frequency of defoliation in the previous growing season (grazing history), and timing of recovery periods on various grassland functional responses in two experiments in western and northwestern Botswana. A field-based clipping experiment at the individual tuft scale demonstrated that perennial grasses are most productive when rested for a full growing season, but that productivity of the highly palatable soft leaved *Brachiaria nigropedata* Fialho & Hiern. decreases exponentially with increasing clipping frequency in the previous season (a lagged effect of grazing history). This species was also more productive in the next season when rested during the early than late growing season. The less palatable needle-leaved *Stipagrostis uniplumis* Licht. ex Roem. & Schult. was less resistant to defoliation than *B. nigropedata* and decreased equally at each clipping frequency regardless of season. A second field-based experiment at the plot scale demonstrated that a full-season recovery period increased tuft densities while its combination with dung increased cover. The effects of hoof trampling on sandy nutrient-poor grasslands appear to be less significant compared with grasslands on fertile soils. Thus, optimal livestock management strategies should aim to promote season-long grazing of both palatable and unpalatable species to disadvantage the less grazing-tolerant unpalatable species and full growing season recovery periods to ensure optimal recovery and future productivity.

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Introduction

The effect of grazing on aboveground net primary productivity (ANPP) has been the subject of much debate for a long time (Westoby 1985; McNaughton 1985, 1993; Belsky et al. 1993; Dyer et al. 1993; Painter and Belsky 1993; Hiernaux and Turner 1996; Knapp et al. 2012). While several studies worldwide demonstrated that large herbivore grazing stimulates grassland productivity, otherwise referred to as *overcompensation* (McNaughton 1979, 1984; Noy-Meiyer et al. 1989;

Turner et al. 1993; Frank et al. 1998), others argued that evidence supporting the concept of overcompensation in grazed swards is inadequate (Westoby 1985; Painter and Belsky 1993; Hiernaux and Turner 1996; Knapp et al. 2012).

However, the nature and effect of grazing are not monodimensional or linear but vary according to the degree of selectivity by grazers (Morris et al. 1992; Fynn 2012), the intensity of grazing (Briske et al. 2008), the nature and evolutionary history of the grasses (tufted versus creeping; long-term history of herbivory) (Milchunas and Lauenroth 1993; Fynn 2012), and the spatial and temporal scales at which grazing occurs (Frank et al. 1998; Fynn 2012). Thus the effects of grazing on grassland productivity cannot be reliably predicted without knowing specific details of the spatial and temporal scale at which grazing occurs and the types of grasses being grazed. For example, moderate levels of grazing generally stimulate grassland productivity in large-scale migratory ecosystems where the effects of grazing are concentrated and transient (McNaughton 1985; Frank et al. 1998) but reduce productivity (undercompensation) in nonmigratory ecosystems where grazing is often nonseasonal and continuous (Milchunas and Lauenroth 1993; Knapp et al. 2012). Nevertheless, at very high levels, grazing generally reduces productivity irrespective of its spatial and temporal scale across

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landscapes (McNaughton 1979, 1985; Turner et al. 1993; Heirnaux and Turner 1996; Owen-Smith 2002).

A strong theoretical and empirical foundation that underlies current scientific understanding of competitive outcomes among plants under differential nutrient loss rates has been established (e.g., Tilman 1988; Berendse et al. 1992; Tomlinson and O'Connor 2004). Heavy continuous grazing runs down nutrient stores in the plant through removal of nutrients and carbohydrates in grazed tissue (Berendse et al. 1992) but, to a lesser degree, carbohydrate stores because grasses are unable to store much carbohydrate (Danckwerts 1993). This compromises the plant's nutrient economy, resulting in reduced tillering and productivity (Berendse et al. 1992; Tomlinson and O'Connor 2004), which is exacerbated by poor root development and inability of plants to access deep-layer soil moisture and growth-limiting nutrients (Hodgkinson and Bass-Becking 1977). Thus, several studies across three continents have demonstrated that grazing in the previous growing season strongly reduced productivity of grasses in the next growing season (Turner et al. 1993; Ash and McIvor 1998; Knapp et al. 1999; Kirkman 2002). Consequently, long-term selective grazing of palatable perennial grasses results in their ultimate death or competitive exclusion by unpalatable species that do not get grazed much (Morris et al. 1992; Anderson and Briske 1995; Dube and Gwarazimba 2000; Fynn 2012).

Most rotational grazing strategies involve a period of grazing of paddocks followed by a period of recovery, with one to several iterations over the growing season. However, the effectiveness of these within-season recovery periods for restoring effective root systems, nutrient stores, and vigor will likely depend on the availability of soil moisture and nutrients for growth and storage in crowns and roots, which can be recycled to aerial growth in the next season. The fact that nutrients are not mineralized evenly over the growing season but rather in pulsed events (Fierer and Schimel 2002), the bulk of which occurs during spring (Scholes and Sanchez 1990; Higgins et al. 2015), suggests that recovery periods during times of good rainfall, especially during the early growing season, will be more effective for grasses than during drier periods or during the late growing season. Much attention has been given to the effect of defoliation frequency and intensity on grass productivity and community composition (e.g., Danckwerts and Nel 1989; Turner et al. 1993; Anderson and Briske 1995; Hiernaux and Turner 1996; Kirkman 2002), but very little attention has been given to the timing of recovery periods in relation to rainfall and nutrient mineralization and this important aspect needs attention.

Apart from the direct effects of grazing, grazing may also have indirect effects on grasslands, such as through its associated trampling effects and dung and urine inputs, which improve forage quality and grassland productivity by increasing rates of nutrient cycling and removing light inhibiting litter (Knapp and Seastedt 1986), as well as promoting seed burial and establishment (McNaughton 1983, 1985; Georgiadis and McNaughton 1990; Frank et al. 1998). Apart from anecdotal evidence (McNaughton 1983) and some experimental studies (e.g., Wilson and Tilman 2002), little attention has been given to the importance of the effects of physical disturbances of the soil surface by trampling in determining community composition through effects on grass seedling recruitment and aerial litter removal. Thus grazing at the right spatial and temporal scale may provide beneficial ecosystem engineering effects that positively influence ecosystem processes and functioning (Jones et al. 1994), which may then lead to feedback effects on plant composition and productivity (McNaughton et al. 1988).

Our study aimed to determine how the frequency of defoliation (simulated grazing by clipping) and timing of recovery periods affect perennial grass productivity and survival, as well as how the indirect effects of grazing via trampling and dung affect grass biomass and cover. Four hypotheses were postulated: 1) Increasing grazing intensity will reduce grass productivity in subsequent seasons, 2) Timing of recovery periods will influence productivity in subsequent seasons, 3) Dung inputs will increase grass and forb biomass and cover, and 4) Clipping, trampling, and dung will have an interactive influence on cover and biomass in grassland communities.

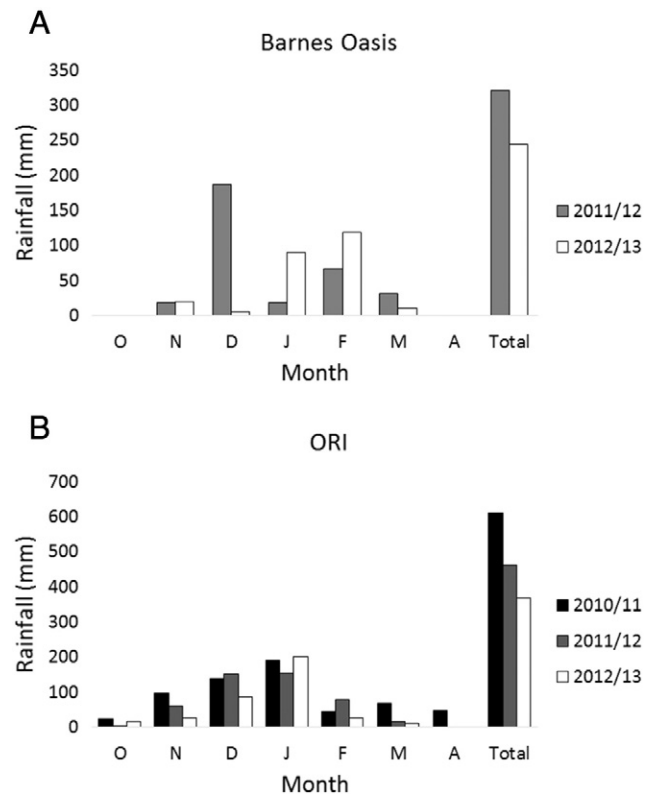


Figure 1. Monthly and annual precipitation data for the 2011/2012 and 2012/2013 growing seasons at the Barnes Oasis ranch in western Botswana (A) and for the 2010/2011–2012/2013 seasons at the Okavango Research Institute (ORI) experiment in north-western Botswana (B).

Source: Barnes Oasis and ORI records.

Materials and Methods

Study Area

The study was conducted in two separate but complementary experiments in Botswana, examining how clipping frequency affects grass productivity and survival. One experiment was conducted at Barnes Oasis ranch located approximately 24 km southeast of Gantsi Township at 21°53'42.17"S and 21°49'53.58"E. The other study site complementing the Gantsi sites was located on the Okavango Research Institute (ORI) campus situated 15 km northwest of Maun at 19°54'19.29"S and 23°31'51.6"E. Maun and Gantsi fall within the Kalahari ecosystem characterized by deep Kalahari sands and hence have slightly variable but comparable conditions.

The climate in the Gantsi area is arid to semiarid with mean monthly winter minimum temperatures of 5°C and summer highs of 33°C (Bhalotra 1987). Mean annual precipitation (MAP) is 430 mm (Botswana Meteorological Services) with the greater proportion

Table 1

Design for clipping treatments for *Brachiaria nigropedata* and *Stipagrostis uniplumis* tufts during the 2011/2012 and 2012/2013 growing season at Barnes Oasis Ranch in western Botswana. X's indicate months when tufts were clipped. Clipping was done once at the end of the month

Treatment	No. clips	Code	2011/2012				2012/2013			
			Dec	Jan	Feb	Mar	Dec	Jan	Feb	Mar
No rest	4	NR	X	X	X	X	X	X	X	X
Early-season rest	2	ESR			X	X			X	X
Late-season rest	2	LSR	X	X			X	X		
Cut once only	1	COF			X				X	
Full-season rest	0	FSR					X	X	X	X

Table 2

Design for clipping, trampling, and dung treatments during the 2010, 2011, and 2012 seasons at the Okavango Research Institute experiment in northwestern Botswana. The crosses indicate the months when treatments were applied

Treatment	Code	2010						2011						2012					
		J	F	M	O	N	D	J	F	M	O	N	D	J	F	M	O	N	D
Clipped twice every year	C1			X			X			X			X			X			X
Clipped twice every alternate year	C2			X			X								X				X
Clipped five times every year	CF	X	X	X		X	X	X	X	X		X	X	X	X	X		X	X
Control (unclipped)	Cont																		
Dung addition	D				X					X							X		
Trampling	T			X	X					X							X		

occurring between October and April (Thomas 2002). About 60% of the rainfall occurs between January and March. Rainfall amount and distribution are variable, resulting in recurring droughts (Cole and Brown 1976; Bhalotra 1987). Although total annual rainfall at Barnes Oasis ranch decreased during the study period (from 2011/2012 to 2012/2013), the area received more rain during the early season (December) in 2011 and during the late season (January and February) in 2013 (Fig. 1A). Maun has a relatively similar climate to Gantsi with a slightly higher MAP of 460 mm (Botswana Meteorological Services). The majority of the rainfall occurs between November and March (Ellery et al. 1990; Ellery et al. 1991). However, there was a decrease in annual rainfall during the study period from 2010 to 2013 (Fig. 1B). Temperatures in Maun are relatively high throughout the year with a mean monthly low of 7°C in winter and a high of 34°C in summer (Botswana Meteorological Services).

The soils in Gantsi and Maun are predominantly Kalahari sands, which typically consist of over 95% sand (Thomas and Shaw 1991) with rare bedrock exposures (Cole and Brown 1976). The sands are mostly deep, structureless, and very low in N, P, and organic matter (Skarpe and Bergstrom 1986; Dougill et al. 1998). Vegetation of the Gantsi area is characterized by open shrub savanna with scattered trees and perennial tufted grasses (Skarpe 1986), where *Terminalia sericea* Burch. ex DC. is a common woody species. The grass layer is dominated by *Stipagrostis uniplumis* and *Digitaria eriantha* Steud. (Cole and Brown 1976; van Oudtshoorn 1999). Vegetation around Maun is characterized by *Colophospermum mopane* Kirk ex Benth. woodland on alluvial soils and with patches of *Terminalia sericea* woodland on deep Kalahari sands (Privette et al. 2004), as in the Gantsi region. Nomenclature for all plant names is according to Germishuizen et al. (2006).

Data Collection

Barnes Oasis Ranch Experiment

Two experimental sites within 2 km of each other (and hence with similar growing conditions), one dominated by *S. uniplumis* and the other by *B. nigropedata*, were identified on Barnes Oasis ranch. These C4 grass species were selected because they are the most dominant species on the ranch (Mudongo 2014) and are good examples of a hard needle-leaved, less palatable species and a soft-leaved, highly palatable species, respectively (van Oudtshoorn 1999). Each experimental site was fenced off with a wire-strand fence with additional fine-mesh chicken wire to protect grasses within the experiment from grazing. The chicken mesh wire was also buried about 20 cm below ground level to keep hares out. The experiment was set up as a random complete block design with 10 blocked replicate tufts of the dominant species at that site. Five clipping treatments (Table 1) were randomly allocated to five tufts of each grass species per block. We selected tufts that were not < 5 cm in basal diameter. Neighboring plants were never close enough to cause shading of experimental tufts and hence were not clipped. Each clipping treatment was denoted by color-coded steel rods, which were used to mark the selected tufts. While clipping was used to simulate grazing by cattle, we realize that cattle rarely graze tufts to low levels, so the clipping represented very intense grazing. All marked tufts were first clipped down (about 5 cm above the

ground) in the dry season (September 2011) to remove senescent material before the growing season for accurate measure of above-ground productivity.

Clipping treatments were done in two growing seasons commencing from December 2011 to March 2012 for the first season and December 2012 to March 2013 for the second season (see Table 1). Tufts were clipped at 5 cm above the ground with the use of clippers. Before the first clipping event, the circumference of each tuft was measured with a flexible measuring tape. This would then be used to calculate the initial tuft area, with productivity being expressed per unit tuft area to standardize comparisons. After each clip, all material was collected in brown paper bags, oven-dried at 60°C for 48 hours, and weighed for biomass. From the treatments that were clipped, productivity was taken as a means of the summed monthly clips in the season.

Productivity in the full season rest (FSR) treatments was measured in the second year by sorting plant material into previous season's dead (oxidized) and current season (green and brown) (e.g., Knapp et al. 2002). Productivity of each surviving tuft was calculated as biomass per initial tuft area to standardize for different tuft sizes. In the first season of the Barnes Oasis ranch experiment, cattle twice managed to break through the fence of the *B. nigropedata* experiment and some experimental tufts were moderately grazed. Owing to the high replication of treatments (10 blocks), however, potential confounding effects of these two grazing events do not seem to have overridden clipping treatment effects, which constituted a far more severe defoliation.

ORI Clipping/Dung/Trample Experiment

Another clipping experiment that had been running in a homogeneous area of grassland at the ORI from November 2009 to February 2013 was used to complement the experiment at Barnes Oasis Ranch. Experimental treatments were applied in the wet seasons of 2009–2010, 2010–2011, and 2011–2012 with assessments of treatment effects being done in 2013. Grazing was simulated by clipping. A three-factor, random, complete block design of 16 treatments replicated seven times to make 112 plots was used in the experiment (four clipping × two soil trampling × two dung addition, Table 2). Plots measured 1.5 × 1.5 m, with 1 m-wide walkways between rows of plots and 0.75-m spacing between plots in a row. The clipping treatments were 1) clipped at the end of December and March every year (C1); 2) clipped at the end of December and March every alternate year (C2); 3) continuously clipped at the end of November, December, January, February, and March every year (CF) (November not clipped if rains came late); and 4) unclipped control (Cont). Soil trampling (T) and dung addition (D) treatments were applied (see Table 2).

In 2010, soil trampling was simulated by chipping the soil surface with an axe but was changed to stamping and breaking the soil with a 6-cm diameter wooden pole (considered similar to the impact of cattle hooves) at the end of March and October in 2010. In 2011 and 2012 it was only carried out in October (see Table 2). Dung inputs involved addition of 200 g of crushed cattle dung per plot, where the amount was calculated from studies of dung deposition in East Africa (David Augustine, unpublished data). An amount equivalent to 6 months of deposition was chosen to represent the time migratory grazers would spend in a seasonal range. Dung inputs were applied just before the

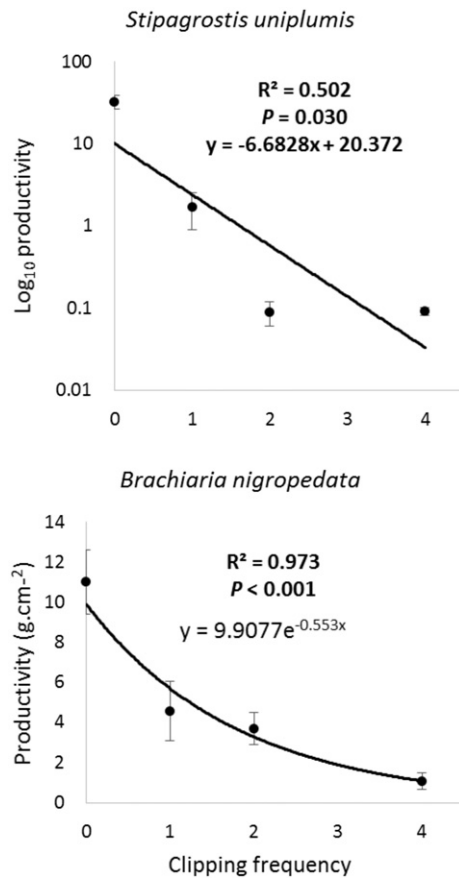


Figure 2. Response of *Brachiaria nigropedata* and *Stipagrostis uniplumis* second-season productivity to first-season clipping frequency during 2011/2012 and 2012/2013 growing seasons at Barnes Oasis ranch in western Botswana. The P values (significant values with $P < 0.05$) and R^2 are from nonlinear and linear (*B. nigropedata* and *S. uniplumis*, respectively) regressions of 50 individuals ($n = 50$) of each species.

soil trampling treatment in October to allow for the effect of trampling on dung incorporation in the soil.

In February 2013 the aerial cover of each grass species and forbs, bare ground, and litter cover, as well as aboveground biomass, were measured in each plot. Tuft density was recorded in each plot by counting the number of grass tufts in a 0.5×0.5 m quadrat placed in the center of each plot (to avoid edge effects). Aboveground biomass was determined by harvesting all plants in the 1-m^2 quadrat and separating into forbs and grass. The aerial cover of each grass species in a plot was determined by giving a visual percentage estimate of its cover within the plot. All harvested plant components (forbs, current-year's grass, and previous-year's dead material) were oven-dried at 60°C for 48 hours and weighed. Rainfall data for the period of the study were obtained from the Barnes oasis and ORI onsite weather stations.

Table 3

Mean (\pm SE) second-year productivity of *Brachiaria nigropedata* and *Stipagrostis uniplumis* under different first-season clipping treatments during the 2011/2012 and 2012/2013 growing season at the Barnes Oasis ranch in western Botswana. Means with a different letter in a column indicate significant differences based on multiple comparisons of Tukey's post hoc test

Treatment	No. Clips	<i>Brachiaria nigropedata</i>	<i>Stipagrostis uniplumis</i>
		Productivity ($\text{g} \cdot \text{cm}^{-2}$)	Productivity ($\text{g} \cdot \text{cm}^{-2}$)
No rest	4	1.08a \pm 0.41	1.98a \pm 0.39
Early-season rest	2	5.29b \pm 1.29	0
Late-season rest	2	2.15a \pm 0.69	0
Cut once only	1	4.57b \pm 1.46	1.72a \pm 0.81
Full-season rest	0	11.0c \pm 1.61	32.8b \pm 6.42

Data Analysis

For both experiments, significance of difference between treatments was obtained by carrying out a linear mixed-effects model (using treatments as fixed effects and block as a random effect) with analysis of variance (ANOVA) and Tukey HSD multiple comparisons in R. At the Barnes Oasis experiment, initial tuft size was used as a covariate in the ANOVA. We tested the effect of clipping frequency in the first season (zero, one, two, or four clips) on second-season productivity of *B. nigropedata* and *S. uniplumis* by performing a nonlinear and linear regression, respectively, on a sample size of 50 individuals of each species ($n = 50$). The control in this analysis (zero clips in first season) was the full-season rest treatment (see Table 1) where previous-year's dead material that had accumulated in the full rest of the first season and was clipped in the December clip of the second season was discarded, as we were only interested in second-season growth. The previous year's dead material (gray in color) could easily be distinguished from second-season growth, which was either live (green) or senesced (brown). After the first clip (December), only second season's growth remained for the January, February, and March clips. Thus, none of our productivity assessments were based on using previous-year's dead material, where some material may be lost through decomposition, which ensured all treatments in the analysis were comparable (second seasons growth only). Normality of the data was tested by Shapiro-Wilk test, whereas homogeneity of variance was checked by examining residuals plots. A binary logistic regression analysis was conducted to predict the odds of survival of tufts using treatment and tuft area as predictors. The test predicts the probability that the dependent variable is either a success or failure using a Wald statistic to assess the significance of coefficients. Data violating assumptions of ANOVA and regression were log transformed.

Results

Barnes Oasis Ranch Experiment

Second-season productivity for both *B. nigropedata* and *S. uniplumis* decreased with increasing first-season clipping frequency, but the decline for *S. uniplumis* was much more abrupt and dramatic at any clipping frequency (see Fig. 2). The full-season rest (FSR) treatment resulted in the highest productivity for both *B. nigropedata* and *S. uniplumis* in the second season (Table 3). A single-cut (COF) treatment reduced productivity of *B. nigropedata* by more than 50% in comparison with the FSR treatment (see Table 3). For *B. nigropedata*, the early-season rest (ESR) treatment resulted in greater productivity than the late-season rest (LSR) treatment despite both treatments having the same clipping frequency (see Table 3).

While clipping treatment did not influence tuft mortality in *B. nigropedata*, the no-rest (NR) and COF treatments made a significant contribution to *S. uniplumis* tuft mortality prediction (Table 4). There were 11% and 44% chances of survival of *S. uniplumis* tufts under the NR and COF treatments, respectively (see Table 4). Tuft area did not influence mortality in either species ($P > 0.05$, see Table 4).

ORI Clipping/Dung/Trample Experiment

Clipping treatment and its interactions with dung and trampling had significant effects on grass cover and tuft density ($P < 0.05$, Table 5). Dung alone did not influence herbaceous vegetation variables ($P > 0.05$, see Table 5) whereas trampling influenced forb cover ($P < 0.05$, see Table 5). Cover of forbs increased from 21.6 ± 3.2 in control treatments to $28.4 \pm 2.96\%$ in trampled treatments. Grass cover was highest ($> 70\%$) in plots clipped in alternate years (receiving a year-long recovery period) and receiving dung (C2D) but was comparable with plots clipped every year combined with trampling and dung additions (C1DT) and those plots clipped in alternate years with dung and trampling (C2DT and C2 each at 61.7%, Table 6). Tuft density was highest in

Table 4

Prediction of survival and death of tufts of *Brachiaria nigropedata* and *Stipagrostis uniplumis* using clipping treatment and tuft area as predictors from the Barnes Oasis experiment in western Botswana. The odds ratios and associated *P* values (significant values with $P < 0.05$ in bold font) are from a binary logistics regression

Predictor	<i>Brachiaria nigropedata</i>						<i>Stipagrostis uniplumis</i>					
	Died	Survived	Wald	EXP (B)	Odds ratio	<i>P</i>	Died	Survived	Wald	EXP (B)	Odds ratio	<i>P</i>
No rest	4	6	0.92	0.38	0.68	0.341	9	1	8.7	0.01	0.11	0.004
Early-season rest	1	9	0.38	2.25	0.92	0.543	5	5	3.2	0.08	0.49	0.052
Late-season rest	0	10	0	NA ¹	0.99	1.000	0	10	0	NA	0.99	1.000
Cut once only	1	9	0.38	2.25	0.92	0.543	6	4	4.4	0.06	0.44	0.033
Full-season rest	0	10	0	NA	0.99	1.000	0	10	0	NA	0.99	1.000
Tuft area	7	53	2.76	1.02	0.80	0.100	21	39	1.88	1.01	0.70	0.172

¹ NA indicates not applicable.

plots clipped in alternate years (C2) and did not differ when dung (C2D) or a combination of dung and trampling (C2DT) was added (see Table 6). Aboveground grass biomass was highest in control plots and lowest in plots clipped and trampled every year (C1T) (Table 7). However, clipping twice every year (C1) and clipping twice every alternate year (C2) yielded comparable grass biomass with the control treatments (see Table 7).

Discussion

Several key results from the tuft clipping experiment on Barnes Oasis Ranch provide important insights and contributions to the debate on grazing effects on compensatory growth in rangelands (e.g., McNaughton 1985; Westoby 1985; Painter and Belsky 1993; Knapp et al. 2012). Our experiment demonstrated that productivity of *B. nigropedata* and *S. uniplumis* decreased exponentially and linearly, respectively, with increasing clipping frequency (see Fig. 2), such that second season productivity was greater for tufts not clipped in the first season (FSR) than tufts clipped in the first season (see Table 3). This is perhaps because by the second growing season the tufts clipped over the first growing season (NR, ESR, LSR, and COF) had incurred reoccurring loss of photosynthetic tissue. Loss of photosynthetic tissue results in losses of photosynthetic-derived carbon and growth-limiting nutrients, which would have been recycled and used for regrowth in the next season (Berendse et al. 1992; Danckwerts 1993; Tomlinson and O'Connor 2004). In addition, frequent and intense grazing may strongly reduce both root biomass and root depth in grasses and sedges (Archer and Tieszen 1983; Danckwerts and Nel 1989; Snyman 2009), which will likely negatively impact nutrient storage and moisture and nutrient uptake for regrowth in the next season. Our clipping height (~5 cm) represented severe defoliation. Thus, our results demonstrate a negative lagged effect of grazing/clipping history on the current season's grassland productivity.

Almost identical results to our experiment were obtained in a clipping experiment in tallgrass prairie, which showed that *Schizachyrium scoparium* Michx. increasingly undercompensated in the second and third growing seasons of clipping (Turner et al. 1993). Relative growth

rates of *Andropogon gerardii* Vitman. were much greater for plants rested in the previous year compared with those grazed in the previous year (Knapp et al. 1999). Similarly, sourveldt grasses grazed in the previous growing season were much less productive in the next season than grasses rested during the previous season (Kirkman 2002), as was the case in Australian grasslands (Ash and McIvor 1998). Thus, although our experimental design does not allow us to examine overcompensation directly, our results suggest that overcompensation will likely only be observed in tufted perennial grasses (not lawn grasses, which are more resilient under grazing owing to lower loss rates) that have had sufficiently long recovery periods after grazing in the previous growing season to enable full recovery of nutrients lost to grazing and development of deep and strong root systems, thereby enabling vigorous regrowth after grazing in the next growing season (reducing lagged effects of grazing history). Under compensation as a result of grazing history, induced lagged effects on productivity were clearly demonstrated by Turner et al. (1993).

Another important result was that *B. nigropedata* showed a seasonal effect of clipping frequency such that tufts rested early in the first growing season, such as in the ESR and COF treatments, were more productive in the second season than tufts rested late (LSR) (see Table 3). This is despite the lower rainfall during the early months (December/January) than later months (February/March) of the 2012/2013 growing season (see Fig. 1). A possible reason for this is that the late growing season is not favorable for grasses to recover nutrients lost to grazing, where peak mineralization may occur in the early growing season (Higgins et al. 2015). This is also linked to the observations that mineralization rates are much higher after rewetting of dry soils (Scholes and Sanchez 1990; Fierer and Schimel 2002), where soils are driest at the start of the early growing season after a long dry season in African savannas. By contrast with *B. nigropedata*, *S. uniplumis* was reduced by each clipping frequency to a similar level irrespective of season, suggesting that *S. uniplumis* is intolerant to severe defoliation at any frequency regardless of season.

While soil moisture may also limit growth in semiarid environments, C4 grasses have an increased water use efficiency that allows them to survive under dry conditions (Edwards et al. 2010), suggesting that early-season nutrient fixation and soil moisture conservation are

Table 5

The main effects of clipping treatment, dung addition, trampling, and their interactions on grass cover, standing biomass, tuft density and forb cover measured during February 2013 at the ORI experiment in northwestern Botswana. The *F* and *P* values (significant values with $P < 0.05$ in bold font) are from an analysis of variance of mixed effects model

Source	<i>Df</i>	Grass cover		Standing grass biomass		Tuft density		Forb cover	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Clipping treatment	3	1.63	0.211	3.13	0.045	13.5	< 0.001	0.14	0.812
Dung	1	0.58	0.463	0.01	0.943	0.45	0.511	0.01	0.980
Trampling	1	1.87	0.200	0.02	0.888	0.01	0.932	5.44	0.041
Clip × Dung	3	3.69	0.033	2.44	0.090	8.92	< 0.001	0.27	0.853
Clip × Trampling	3	5.49	0.011	3.40	0.041	8.23	< 0.001	0.81	0.500
Dung × Trampling	1	1.62	0.230	1.57	0.233	0.03	0.864	2.77	0.131
Clip × Dung × Trampling	3	9.65	< 0.001	0.47	0.700	5.23	0.010	0.98	0.420

Table 6

Mean (\pm SE) grass cover and tuft density in response to clipping and its interactions with dung and trampling measured during February 2013 at the Okavango Research Institute experiment in northwestern Botswana. Means with a different letter in a column indicate significant differences ($P < 0.05$) based on multiple comparisons of Tukey's post hoc test. Only those treatments with significant effects are shown

Treatment	Grass cover (%)	Tuft density ¹ (no. \cdot m ⁻²)
Clipped twice every year (C1)	55.8c \pm 1.05	17.0c \pm 0.24
Clipped twice every alternate year (C2)	61.7dc \pm 1.16	18.9d \pm 0.33
Clipped five times every year (CF)	53.1bc \pm 1.00	16.3bc \pm 0.29
Control (Cont)	39.3a \pm 0.74	14.8a \pm 0.18
C1 \times Dung (D)	55.9c \pm 1.05	16.9c \pm 0.25
C2 \times D	72.7d \pm 1.37	18.9d \pm 0.35
CF \times D	51.9bc \pm 0.98	16.1b \pm 0.30
Cont \times D	47.1ab \pm 0.88	14.7a \pm 0.22
Cont \times Trample (T)	27.6a \pm 0.60	15.1a \pm 0.25
C1 \times D \times T	63.0dc \pm 1.19	18.0c \pm 0.44
C2 \times D \times T	61.7dc \pm 1.16	19.1d \pm 0.36
CF \times D \times T	56.0c \pm 1.06	16.3bc \pm 0.29
Cont \times D \times T	26.7a \pm 0.64	15.5ab \pm 0.30

¹ Values were log transformed for statistical analysis.

critical in dry, nutrient-poor environments. This is a key and novel result that links grass productivity under clipping to the timing of rest during the growing season, which has not been demonstrated in previous studies, particularly in sandy dystrophic soils.

We suggest that N economy in grasses provides a unifying explanation of our observations on grazing history effects and timing of resting/grazing on the next growing season's productivity because both of these factors likely affect N uptake and storage (grazing removes N, while early season resting falls in the period of peak N mineralization), but this will require further investigation. For example, dry season grazing, when grasses are dormant and have translocated N to below ground stores, has much less negative effect on productivity in the next season compared with wet season grazing, where grasses would lose more N to grazing (Ash and McIvor 1998). Similarly, grassland productivity can be linked to as far back as the previous 4 years' rainfall events (Wiegand et al. 2004), which control mineralization pulses in soils (Scholes and Sanchez 1990; Fierer and Schimel 2002; Higgins et al. 2015).

The other key finding of our experiment was that the palatable *B. nigropedata* was much more tolerant of clipping than the less palatable *S. uniplumis* (see Table 4) as observed in clipping experiments comparing palatable and unpalatable species in North America (Anderson and Briske 1995) and South Africa (Morris and Tainton 1993). More preferred palatable grasses such as *B. nigropedata* may be more tolerant of clipping than tough-leaved grasses such as *S. uniplumis*, but they are often replaced by these less preferred grasses under poor grazing management practices (Morris et al. 1992; Anderson and Briske 1995). The palatable grasses are selectively eaten and overgrazed, which, as we demonstrated, leads to declining

Table 7

Mean (\pm SE) standing grass biomass in response to clipping and its interactions with trampling measured during February 2013 at the Okavango Research Institute experiment in northwestern Botswana. Means with a different letter in a column indicate significant differences ($P < 0.05$) based on multiple comparisons of Tukey's post hoc test. Only those treatments with significant effects are shown

Treatment	Standing biomass ¹ (g \cdot m ⁻²)
Clipped twice every year (C1)	71.7abc \pm 1.66
Clipped twice every alternate year (C2)	72.5bc \pm 1.78
Clipped five times every year (CF)	71.0ab \pm 1.82
Control	76.5c \pm 1.33
C1 \times Trample (T)	67.4a \pm 1.48
C2 \times T	69.7ab \pm 1.52
CF \times T	70.6ab \pm 1.92
Control \times T	77.4c \pm 1.42

¹ Values were log transformed for statistical analysis.

productivity and ultimately replacement by less preferred species (Morris et al. 1992; Anderson and Briske 1995). However, grasses that are adapted to a lack of disturbance in the form of grazing or fire have developed tolerance traits such as slow growth rates and shade tolerance to enable them to withstand reduced light levels and increased litter (MacDougall and Turkington 2004; Fynn et al. 2011) but are less tolerant of clipping/grazing (Morris and Tainton 1993).

The similarity of the results of our study with several others on grazing history (Turner et al. 1993; Ash and McIvor 1998; Knapp et al. 1999) and life history (Morris and Tainton 1993; Anderson and Briske 1995) effects on grassland productivity, despite regional and intercontinental separation and different grass species dominants, demonstrates that grazing history and life history effects are key general factors that need to be accounted for in understanding grassland productivity responses to grazing. Thus, we suggest that when taking into account 1) the length of recovery after clipping/grazing (short-term grazing history), 2) the evolutionary history (grazing tolerance), and 3) the life history (palatable, soft leaved vs. unpalatable, needle leaved) of the dominant grass, the compensatory response of grasslands (overcompensation vs. undercompensation) under grazing becomes a robust and predictable concept. These results support hypotheses 1 and 2.

In accordance with our findings that season-long resting (alternate year clipping) increased grass productivity, at the ORI experiment we demonstrated that alternate-year clipping (C2) increased tuft densities irrespective of dung addition and trampling, whereas grass cover increased when dung was added (see Tables 5 and 6). While soil trampling has been found to increase seedling establishment (Wilson and Tilman 2002) and hence high seedling densities (McNaughton 1983), this was not the case in our study. A possible explanation of this difference is that our study was conducted in sand veld environments, where the effects of hoof trampling may be less pronounced than on hard veld environments.

Although no attention was paid to the soil type in terms of its inherent pattern of nutrient availability, the response is interpreted to have taken place in poor sands on which the rates of regrowth are accordingly expected to be slow—grasses on more fertile soils may have been less susceptible to mortality under clipping than on these sandy soils, but it is expected that productivity responses to clipping history would have been the same (e.g., Turner et al. 1993; Kirkman 2002).

Implications

Our results confirmed that a full growing season recovery period is far superior to partial resting within the growing season, as noted elsewhere by Kirkman and Moore (1995), Zacharias (1995), and Briske et al. (2011). The observation that even one cut during the growing season reduced productivity in the next growing season by half relative to a full growing season recovery suggests that partial recovery periods (early or late growing season recovery periods) are not optimal in semi-arid, nutrient-poor rangelands but rather that a full growing season recovery period is the best management strategy in these rangelands.

Most rotational grazing systems worldwide include several grazing and recovery periods within each paddock over the growing season. Our data suggest that rotational resting (deferred resting) in which some paddocks are grazed and others rested over the entire growing season (e.g., Kirkman and Moore 1995) is a superior approach to grazing management. However, this may be relative to plant productivity of C4 bunch grasses and limited to the environmental conditions characterizing sandy nutrient-poor rangelands, although other studies on fertile soils and under high rainfall have drawn the same conclusions (Zacharias 1995). Our observations that less palatable, needle-leaved grasses were less tolerant of clipping than palatable soft-leaved grasses suggests that managers can aim to reduce the abundance of less palatable grasses by use of nonselective grazing techniques, which encourage grazing of both palatable and unpalatable species (e.g., season-long

grazing after fire to maintain unpalatable grasses in a short, higher-quality state).

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