

Challenges of foraging on a high-quality but unpredictable food source: the dynamics of grass production and consumption in savanna grazing lawns

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Summary

1. Grazing lawns are short grassland areas where intense grazing maintains grass in an early growth stage. These areas represent a source of high-quality forage for herbivores. However, as herbivores continually remove nearly all the newly accumulated biomass, instantaneous resource availability depends on the dynamics of grass growth.

2. In this study, we investigate how production and consumption inside grazing lawns are synchronized. We then explore how that synchronization affects the ability of large herbivores to use these lawns. We also provide a critical comparison between grazing lawns and intensively managed grasslands in livestock farms.

3. We investigated vegetation production and herbivore grazing activity during a wet and a dry season using clipping experiments and direct observation in two grazing lawns in a South African savanna.

4. Weekly total grazing activity by unit area was strongly and positively related to short-term primary production. This indicates a close synchronization between these two processes. In contrast, grazing activity was poorly related to standing biomass. Primary production had a threshold response to the weekly pattern of rainfall, implying a stochastic dynamics of grass growth.

5. The dynamics of grass production and consumption of grazing lawns is similar to the one of continuously stocked grazing systems from intensively managed grasslands. But the mechanisms regulating the two systems lead to different equilibrium points between production and consumption. The two systems also have opposed nutritional functions within the animal diet.

6. *Synthesis.* The close synchronization between resource production and consumption inside grazing lawns indicates that instantaneous resource availability is a direct function of the short-term rate of grass growth. In tropical savannas, the main source of variability of lawn grass primary productivity is the stochastic nature of short-term rainfall. As a result, herbivores' ability to use grazing lawns is poorly predictable in time. This has important consequences on the degree of information herbivores can use in the elaboration of their foraging strategies, and on the potential interest of grazing lawns.

Key-words: climatic variability, continuous stocking, grazing systems, intensively managed grasslands, large herbivores, primary production, rainfall, white rhino

Introduction

Sustainable food resource use is critical in plant–herbivore systems supporting intense levels of consumption. At a regional scale, vertebrate herbivores from most native terrestrial ecosystems only remove a limited proportion (10–20% on

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average) of the annual net above-ground primary production (NAPP) (Wiegert & Evans 1967). At a local scale, however, levels of consumption can be much higher. By enhancing local resource attractiveness, repeated grazing can lead to the formation of intensively grazed, short-cropped sward areas called grazing lawns (McNaughton 1984). Grazing lawns exist in a large variety of terrestrial ecosystems, including North-American tall or mixed grass prairies (Coppock *et al.* 1983; Knapp *et al.* 1999), European grasslands (Menard *et al.* 2002), alpine tundra (McIntire & Hik 2002), subarctic salt marshes (Person *et al.* 2003) and African savannas (Vesey-Fitzgerald 1965; McNaughton 1984). In these lawns, herbivores can consume up to 80–95% of the annual NAPP (e.g. McNaughton 1985; Person, Babcock & Ruess 1998). Such intense levels of consumption involve a dynamics of resource production and consumption completely different from that in less intensively grazed areas. Understanding this dynamics is of critical importance for evaluating the potential interest of large herbivores in grazing lawns as a food resource.

Grazing lawns are generally reported to be highly profitable grazing areas (e.g. McNaughton 1984; Person *et al.* 2003; Verweij *et al.* 2006). Maintaining a short-cropped sward allows herbivores to keep grass tissues in a phenologically young state of high nutritional value (Waite 1963). In addition, primary production remains at remarkably high levels, sometimes exceeding 10 tonnes dry matter ha⁻¹ year⁻¹ in tropical areas (McNaughton 1985). However, continually removing nearly all NAPP has a strong impact on instantaneous food availability: it does not allow the build up of standing crop. As a result, the ability of herbivores to use grazing lawns at any one time is probably strongly dependent on the short-term rate of primary production of these areas.

Results from past studies have emphasized the importance of temporal changes in primary production on the pattern in which herbivores use grazing lawns. For instance, in the Serengeti Plains (Tanzania), the localized distribution of rainfall leads to levels of primary production that are highly stochastic in space and time (McNaughton 1985). Nomadic populations of Thomson's gazelle (*Gazella thomsoni*) and wildebeest (*Connochaetes taurinus*) closely track these changes in the large-scale spatial distribution of lawn grass production (Wilmschurst *et al.* 1999; Fryxell *et al.* 2004). But at a more local scale, the temporal link between primary production and grass consumption in grazing lawns remains poorly documented.

Continuously stocked grazing systems, optimized for live-stock production in intensively managed grasslands, have a dynamics of grass production and consumption remarkably similar to the one of grazing lawns. Indeed, they were designed to maintain a relatively constant short sward canopy by letting domestic herbivores continually remove newly accumulated biomass (Spedding 1965). Whereas the two systems remain fundamentally different in their overall functioning (i.e. continuously stocked grazing systems are closed and carefully managed by farmers, whereas grazing lawns are open, with herbivores free to move in and out), established fine-scale processes on the dynamics of grass production and consumption in intensively managed grasslands (e.g. Bircham & Hodgson

1983; Parsons *et al.* 1983; Johnson & Parsons 1985) can usefully enlighten patterns observed in grazing lawns.

The objective of this study was first to determine the strength of the temporal link between primary production and grass consumption inside grazing lawns. Secondly, it was to evaluate how this link affects the ability of large herbivores to use grazing lawns as a food resource. Specifically, we determined for grazing lawns the relationships at a weekly time-scale between: (i) primary production and rainfall, (ii) large herbivore grazing activity and primary production, and (iii) large herbivore grazing activity and standing biomass. We interpret and discuss our results relative to the principles of grass production and consumption established in continuously stocked grazing systems in farms and provide a critical analysis of this comparison. We then discuss implications of our results in a context of highly stochastic distribution of rainfall.

Materials and methods

STUDY SITE

We conducted the study in the Hluhluwe section (hereafter Hluhluwe) of the Hluhluwe-iMfolozi Park (28°10' S, 32°00' E), an enclosed c. 90 000-ha mesic savanna in South Africa. Mean annual rainfall ranges from 750 to 950 mm, depending on altitude. Inter-annual variations in monthly rainfall are high during the wet season (CV from 55% to 75% mm) and even higher during the dry season (CV from 74% to 154%).

The vegetation comprises open grasslands, savannas, broad-leaved thickets and *Acacia* woodlands (see Whateley & Porter (1983) for a detailed description). Grazing lawns occur as small patches (mostly < 8 ha) in a taller bunch-grass matrix and cover < 10% of the total area of the Park (Archibald *et al.* 2005). Grass species in grazing lawns include, in order of abundance, *Digitaria longiflora*, *Dactyloctenium australe*, *Sporobolus nitens*, *Digitaria eylesii* and *Eustachys paspaloides*. Indigenous large grazers include white rhino (*Ceratotherium simum*), African buffalo (*Syncerus caffer*), zebra (*Equus burchelli*), blue wildebeest (*Connochaetes taurinus*), warthog (*Phacochoerus africanus*) and impala (*Aepyceros melampus*). Populations are resident. Herbivore biomass in Hluhluwe (c. 11 000 kg live weight km⁻², Ezemvelo KwaZulu-Natal Wildlife data) is high in comparison with other African conservation areas with the same range of rainfall (Fritz & Duncan 1994). White rhinos (c. 480 individuals in 2006) account for around 30% of this biomass and are the main actors of the maintenance of grazing lawns (Waldram, Bond & Stock 2008).

We conducted the study in two distinct grazing lawns (site 1: 2.5 ha; site 2: 6.6 ha), 7 km apart from each other, during both the dry (July–August 2005) and wet (January–March 2006) seasons. Daily rainfall data come from four automatic meteorological stations located nearby our study sites.

PRIMARY PRODUCTION

We used net biomass accumulation (NBA, g m⁻² day⁻¹) instead of NAPP as a measure of primary production. NBA corresponds to NAPP minus the rate of tissue death and provides better estimates of newly produced biomass available to herbivores. We monitored short-term NBA of lawn grass by repeatedly clipping grass inside small enclosures. Four enclosure replicates of 2 × 2 m were randomly placed in each of the two sites, and six square 0.5-m² plots were

arranged evenly in each of them. Each enclosure had a balanced factorial design with two levels of clipping height (2 and 6 cm) and three levels of clipping frequency (weekly, every 1.5 weeks, and every 3 weeks). Treatments (two clipping heights \times three clipping frequencies) were randomly arranged in each enclosure. This design allowed the simulation of a variety of grazing intensities, as well as monitoring the dynamics of lawn grass production at different time-scales (from 1 to 3 weeks). We chose clipping heights of 2 and 6 cm to simulate the mean cropping height of white rhino and zebra, respectively. As sward height was extremely short (1–2 cm) and without any growth at the beginning of the dry season, we limited our clipping to the 2-cm clipping treatment throughout this season. Clipped samples were oven-dried at 60 °C for 8 h to obtain dry mass.

STANDING BIOMASS

We divided each site into 12 areas of relatively homogeneous size and vegetation aspect (sward height, presence of bunch grasses or shrubs). During the dry season, three locations were randomly selected in each area and for each sampling event (three by site). Sampling consisted of clipping all standing material within a 60 \times 60 cm quadrat. During the wet season, grazing lawn swards were much more heterogeneous. Thus, we used transects (dimensions 0.1 \times 10 m) rather than quadrats to sample the vegetation during this period. One location was randomly selected inside each area and for each sampling event (three for site 1, two for site 2). Due to safety problems (e.g. presence of lions and elephants), we were not able to complete a third sampling event on site 2 at the end of the study. Transect were chosen along a random direction from the selected location. Because of the change of sampling procedure between the dry and the wet season, we did not try to compare standing biomass between the two seasons. It was clear, however, that standing biomass was higher during the wet than during the dry season. Vegetation samples were sorted by species and tissue type (i.e. green leaves, dead leaves and stems) before they were oven-dried.

GRAZING ACTIVITY

We monitored grazing activity of all herbivore species present on the lawns by direct observation during daylight hours (6:00–18:00 hours). We conducted observations from hides installed in a tree at the centre of each site. This insured minimal disturbance of the feeding behaviour of observed herbivores. Every 5 min, we counted the number of individuals present for each species, and classified them according by age, sex and activity (young or adult, male or female, grazing or not). Grazing activity ($\text{min kg}^{0.75} \text{ha}^{-1}$) was calculated as the product of the total time spent grazing by each individual and its metabolic body mass ($\text{BM}^{0.75}$), divided by the area of the site. This was done to allow interspecific and inter-site comparisons. We made a distinction in the mean body mass of age–sex classes for white rhinos (adult males: 2200 kg, adult females: 1700 kg, young: 400 kg, from Owen-Smith 1988) and warthogs (adult males: 90 kg, adult females: 70 kg, young: 10 kg, from Brooks & MacDonald 1983) only, as these differences were significant for these two species. We used a unique body mass value for other species: zebra, 230 kg; wildebeest, 220 kg; impala, 50 kg (from Brooks & MacDonald 1983).

During the dry season, we conducted 12 observation hours a week at each site over seven consecutive weeks. Observations were divided into three sessions of 4 h (a morning, a mid-day and an afternoon) conducted at random during the week. During the wet season, grazing activity was much more intense. As a result, we conducted continuous observations (12 h every day for two or three consecutive

weeks). The two sites were observed alternately in the following sequence: site 1 (2 weeks), site 2 (2 weeks) and site 1 (3 weeks). We were not able to complete additional observations on site 2 at the end of the study due to safety problems.

DATA ANALYSIS

The clipping experiment used to monitor NBA had a hierarchical sampling design (enclosures were nested within sites) and temporal pseudo-replication between successive clipping events. We used mixed generalized linear models to test covariates and treatments affecting NBA. As values for NBA were strictly positive with a variance increasing roughly proportionally with the mean, we used a quasi-Poisson distribution in the models, as suggested by Fisher (1949). We used two different models to test effects on NBA under the weekly clipping treatment. The first model used data from the two seasons, with cumulative rainfall over 1 week (CRain1) and season (Season) as fixed effects. The second model was restricted to data from the wet season. Fixed effects were CRain1, time in days since the beginning of drier conditions, i.e. since the last big rainfall of January (Drier, see Fig. 1b) and clipping height (Ch). We used a third model, restricted to the wet season, to test effects on NBA at a time-scale of 3 weeks. This allowed us to test the effect of clipping frequency (Cf) by pooling over 3-week data from plots with shorter clipping intervals. Fixed effects for this last model were cumulative rainfall over 3 weeks (CRain3), Ch and Cf. All three models contained two additive terms as random effects. One for the nested hierarchical design with enclosure nested within site, and the other with the number of successive clipping events. Non-significant interactions were systematically removed during the model simplification procedure. We tested for significant differences in standing biomass by using linear models with log-transformed biomass data. Finally, we used a Spearman rank correlation test to investigate correlations of grazing activity with NBA and standing biomass. All analyses were conducted on R 2.7.0. GUI 1.24 free online software (<http://www.R-project.org>).

Results

PRIMARY PRODUCTION

Net biomass accumulation closely matched the rainfall pattern during both the wet and the dry seasons (Fig. 1a–f). Over the two seasons, the 1-week cumulative rainfall positively influenced NBA from the weekly clipping treatment (Table 1, model 1, estimate = 0.165 ± 0.016). This relationship had a marked threshold shape (Fig. 2). Weekly NBA remained close to zero for cumulative rainfall lower than 14 mm, whereas it increased linearly for higher rainfall values. Season did not have a significant effect on this relationship (Table 1, model 1). During the wet season, the number of days since the beginning of drier conditions (i.e. since the last big rain of January) had an additional negative effect on weekly NBA (Table 1, model 2, estimate = -0.056 ± 0.007). On the other hand, clipping height did not have any significant effects (Table 1, model 2).

Considering a time-scale unit of 3 weeks, the relationship between NBA (from the three clipping frequencies) and cumulative rainfall was no longer significant (Table 1, model 3); neither was clipping height nor clipping frequency (Table 1,

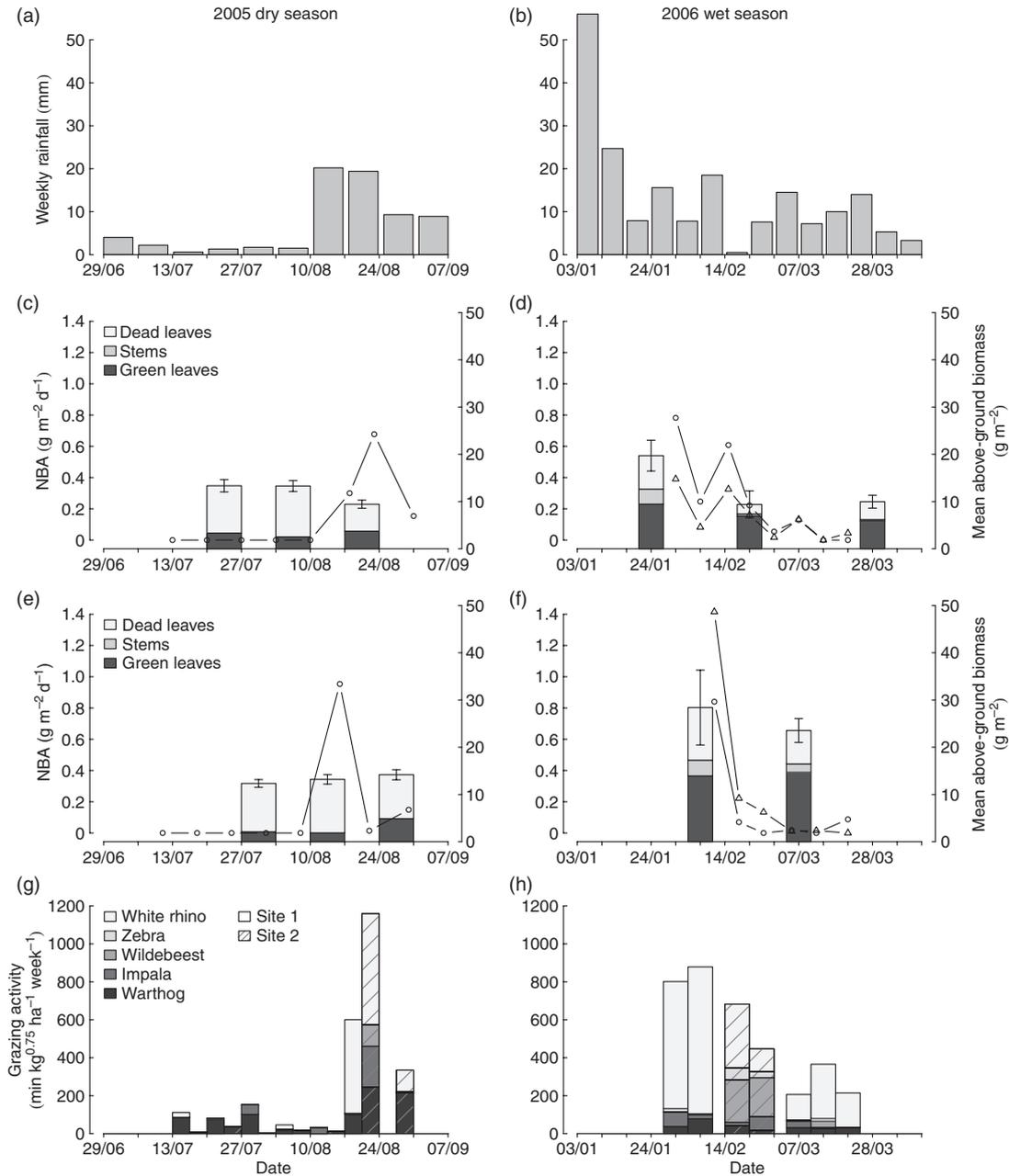


Fig. 1. Dynamics of monitored grazing lawns during the 2005 dry season (left column) and the 2006 wet season (right column). X-axis ticks correspond to 1 week. (a,b) Weekly rainfall (mm). (c–f) Solid lines: net biomass accumulation (NBA, $\text{g m}^{-2} \text{day}^{-1}$) from clipping experiment (\circ clipping height = 2 cm, \triangle clipping height = 6 cm). Only weekly clipping frequency is presented. Histogram bars: mean standing biomass (g m^{-2} , \pm SE of total biomass). (c) and (d) are results for site 1, (e) and (f) for site 2. (g,h) Total grazing activity during day hours over 1 week in minutes spend grazing \times kg of metabolic body mass ($\text{BM}^{0.75}$) by ha for each observed species.

model 3). The absence of effect of clipping frequency indicates that NBA was a strictly additive process between 1 and 3 weeks. A time-scale of 1 week is therefore likely to better capture the effect of a heterogeneous rainfall distribution on NBA.

STANDING BIOMASS

The biomass of green leaves was generally low during the dry season (Fig. 1c,e). However, it significantly increased at the third sampling event (site 1: $F_{2,73} = 7.77$, $P < 0.001$, con-

trast: $t = 2.67$, $P = 0.009$; site 2: $F_{2,55} = 15.45$, $P < 0.001$, contrast: $t = 5.17$, $P < 0.001$), after the heavy rains of mid-August. During the wet season (Fig. 1d,f), total biomass ($F_{1,54} = 15.24$, $P < 0.001$) and green leaf biomass ($F_{1,54} = 14.15$, $P < 0.001$) were significantly higher on site 2 than on site 1. For site 1, total biomass significantly decreased between the three sampling events ($F_{2,26} = 3.69$, $P = 0.038$), but green leaf biomass remained constant ($F_{2,26} = 1.08$, $P = 0.35$). For site 2, neither total ($F_{1,18} = 0.12$, $P = 0.73$) nor green leaf biomass ($F_{1,18} = 0.18$, $P = 0.68$) significantly changed between the two sampling events.

Table 1. Analysis of variance from mixed generalized linear models for effects of environmental conditions and treatments on net biomass accumulation. Covariates (fixed effects) – CRain1, cumulative rainfall over 1 week; CRain3, cumulative rainfall over 3 weeks; Drier, number of days since the beginning of drier conditions (i.e. since the last big rain of January). Factors (fixed effects) – Season, studying period (wet or dry season); Ch, clipping height (2 or 6 cm); Cf, clipping frequency (weekly, every 1 week and half, and every 3 weeks)

Source of variation	d.f.	Deviance	χ^2	<i>P</i> -value
Model 1: two seasons, weekly clipping treatment only				
CRain1	1	30.53	20.08	< 0.001
Season	1	0.01	0.01	0.92
Model 2: wet seasons, weekly clipping treatment only				
CRain1	1	14.79	7.07	0.008
Drier	1	9.56	11.13	< 0.001
Ch	1	0.01	0.01	0.93
Model 3: wet seasons, all three clipping treatments				
CRain3	1	0.70	0.62	0.43
Ch	1	0.71	0.74	0.39
Cf	2	0.07	0.07	0.96

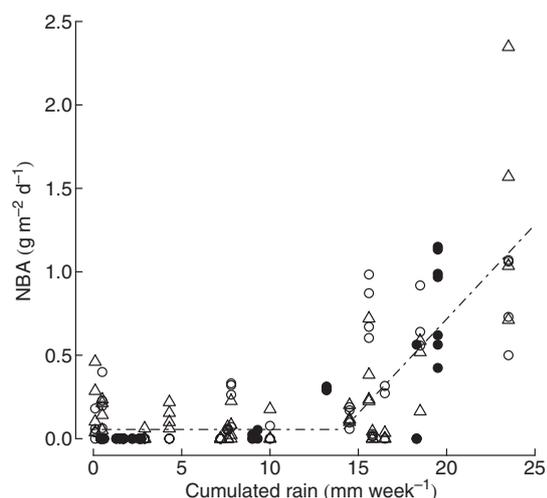


Fig. 2. Relationship between lawn grass net biomass accumulation (NBA, $\text{g m}^{-2} \text{day}^{-1}$) at the weekly clipping frequency and cumulative rainfall (mm week^{-1}) over the 7 days preceding the clipping event. • Dry season, 2-cm clipping treatment; ○ wet season, 2-cm clipping treatment; △ wet season, 6-cm clipping treatment. Dashed line is the linear threshold function minimizing deviance of fitted values: $\text{NBA} = 0.055$ for cumulative rainfall $< 14.14 \text{ mm week}^{-1}$, and $\text{NBA} = 0.11X - 1.54$ for cumulative rainfall $> 14.14 \text{ mm week}^{-1}$.

GRAZING ACTIVITY

Grazing activity closely matched variations of weekly NBA over time (Fig. 1). During the dry season (Fig. 1g), herbivores rarely used grazing lawns prior to the heavy rains of August. After these rains, primary production increased and green leaves re-appeared. As a result, herbivores moved back onto these lawns and total grazing activity reached its highest levels. During the wet season (Fig. 1h), both total grazing activity

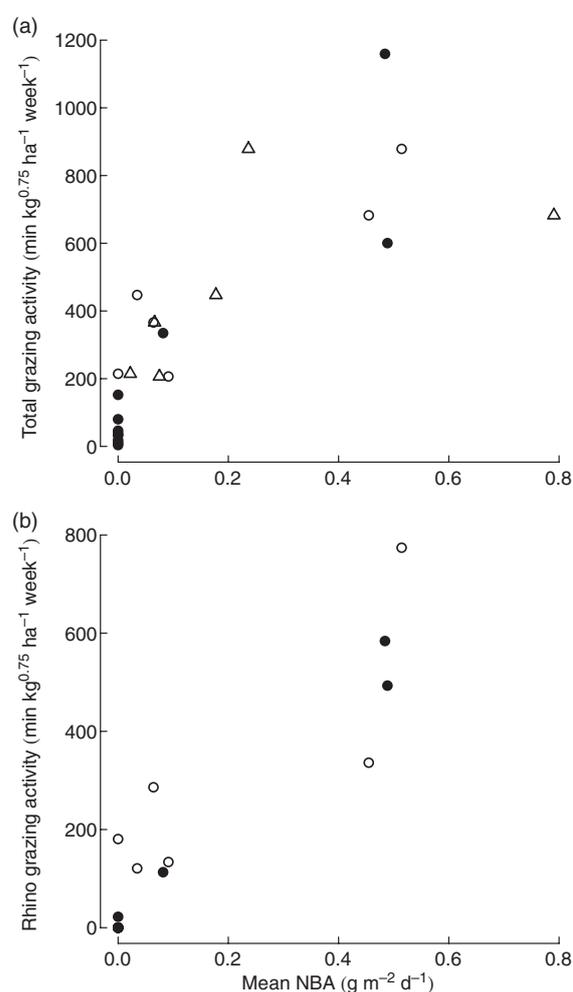


Fig. 3. Relationship between grazing activity over 1 week in minutes spent grazing $\times \text{kg}$ of metabolic body mass ($\text{BM}^{0.75}$) by ha, and mean net biomass accumulation (NBA, $\text{g m}^{-2} \text{day}^{-1}$) of lawn grass from the weekly clipping treatment over the week of and before the grazing activity observations. (a) Total grazing activity for all species, (b) grazing activity for white rhino only. • Dry season, 2-cm clipping treatment; ○ wet season, 2-cm clipping treatment; △ wet season, 6-cm clipping treatment.

and weekly NBA declined over time, whereas standing green biomass remained constant.

Considering weekly NBA over the week of and before the grazing observations, weekly total grazing activity and NBA were strongly correlated for the 2-cm clipping treatment (Fig. 3a, Table 2). Correlation was not significant for the 6-cm clipping treatment (Table 2), probably because of the low number of replicates. It followed, however, the same trend as the 2-cm clipping treatment (Fig. 3a). Considering each herbivore species independently, the relationship at the 2-cm clipping height was significant for white rhino (see Fig. 3b), wildebeest and warthog, nearly significant for impala and not significant for zebra (Table 2).

Total grazing activity over 1 week was positively correlated to standing green biomass during the dry seasons ($r_s = 0.94$, $P = 0.017$, $N = 6$), but not during the wet season ($r_s = 0.3$, $P = 0.68$, $N = 5$).

Table 2. Spearman rank correlation test between grazing activity over 1 week and weekly net biomass accumulation over the week of and before the grazing observations. Clipping height is the clipping treatment used for the measurements of net biomass accumulation

Herbivore species	Clipping height (cm)	<i>N</i>	Total observed grazing time (min)	r_s	<i>P</i> -value
All	2	17	15 565	0.86	<0.001
All	6	6	15 565	0.77	0.10
White rhino	2	17	4015	0.89	<0.001
Wildebeest	2	17	1655	0.71	0.001
Warthog	2	17	6135	0.54	0.024
Impala	2	17	2710	0.46	0.057
Zebra	2	17	1050	0.37	0.147

Discussion

Many studies have reported that grazing lawns are important areas of highly nutritive food for grazing herbivores (e.g. McNaughton 1984; Person *et al.* 2003; Verweij *et al.* 2006). However, our results show that grazing activity inside lawns is strongly dependent on the short-term rate of primary production of these areas. As a result, the ability of herbivores to use these lawns depends on the sustainability of grass growth. We also found that primary production of grazing lawns had a threshold response to weekly rainfall. This dependence of grazing lawns' primary production on a process as stochastic as short-term rainfall indicates that grazing lawns are, in arid to mesic areas, highly unpredictable resources in time. This makes their exploitation by herbivores unsustainable, particularly for resident populations who cannot migrate to track grass productivity.

DETERMINANTS OF GRAZING ACTIVITY IN LAWNS

Weekly total grazing activity was strongly and positively related to short-term NBA (Fig. 3a). On the other hand, it was poorly related to standing green biomass. Indeed, both NBA and total grazing activity significantly decreased during the wet season, whereas standing green biomass remained constant (Fig. 1). During the dry season, August rainfall resulted in a strong increase of both NBA and total grazing activity. Despite lower standing green biomass, NBA and grazing activity reached values near the ones observed at the beginning of the wet season (Fig. 1). It is, however, possible that this last pattern was due to the attractiveness of fresh, green leaves being greater during the dry season than during the wet season.

We found a strong positive correlation between grazing activity and standing green biomass during the dry season. This result does not contradict our finding that grazing activity was poorly related to standing green biomass. It only reflects the contrast between conditions in early dry season, when standing green biomass was too low to support grazing activity, and conditions at the end of the dry season, when an increase in standing green biomass allowed grazing activity. As

soon as there was enough biomass to support grazing, grazing activity and standing green biomass were no longer related.

By adjusting their grazing activity to primary production, large herbivores maintain grazing lawns in a dynamic equilibrium where newly produced biomass is continually consumed, and where standing biomass remains relatively constant. Studies from salt marshes in northern Netherlands (Ydenberg & Prins 1981) reported similar results. On a range of lawns supporting widely different rates of primary production, barnacle geese (*Branta leucopsis*) were able to maintain an equal standing biomass by grazing more on sites that were more productive.

These findings strongly suggest that the ability of large herbivores to use grazing lawns is driven by short-term primary production rather than standing biomass. The recrudescence of grazing activity after the large rainfall event observed during the dry season confirms that primary production is the determinant of grazing activity, and not grazing activity the determinant of primary production. As a result, environmental conditions affecting the pattern of primary production over time will be the ultimate drivers of the ability of herbivores to use grazing lawns.

DEPENDENCE OF PRIMARY PRODUCTION ON THE PATTERN OF RAINFALL

In accordance with the vast majority of studies from grasslands or savanna (e.g. Rosenzweig 1968; Sala *et al.* 1988; O'Connor, Haines & Snyman 2001), we found a strong relationship between rainfall and primary production. Perhaps more interesting is that this relationship was highly significant at the time-scale of 1 week but not when we looked over 3 weeks. The threshold response of NBA to weekly rainfall (Fig. 2) can explain this discrepancy. When summed over 3 weeks, rainfalls lower than this threshold (no production) counteract rainfalls higher than the threshold (high production), blurring the relationship.

The close synchronization between rainfall and primary production, and the threshold shape of this relationship have important implications. Ultimately, it indicates that grazing lawns are productive areas only when weekly rainfall exceeds the threshold value. Short-term productivity is thus not sustained over time because of high rainfall stochasticity. Using the threshold value, we can predict from historical rainfall data the expected temporal pattern of lawn grass production over the year in Hluhluwe (i.e. when weekly rainfall exceeded 14 mm). In 2002, a particularly dry year, weekly cumulative rainfall exceeded 14 mm for only 71 days, compared to 138 days in 2005, which was an average rainfall year (Fig. 4). We can compare this difference in the number of days of potential lawn grass production (i.e. $\times 2$) to the difference in the annual rainfall between 2002 (480 mm) and in 2005 (763 mm) (i.e. $\times 1.6$). The intra-seasonal distribution of rainfall events may therefore have an effect on primary production as important as the annual amount of precipitation, a result already pointed out in recent studies (Knapp *et al.* 2002; Swemmer, Knapp & Snyman 2007). Another implica-

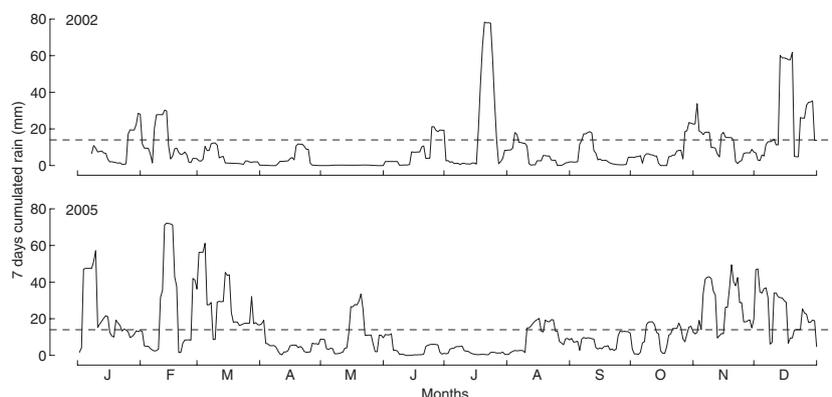


Fig. 4. Daily variation of cumulative rainfall (mm) over seven preceding days in Hluhluwe during two contrasted years (an exceptionally dry year: 2002, and an average rainfall year: 2005). Dashed line represents the threshold of weekly cumulative rainfall (14 mm) allowing a significant primary production of grazing lawns. A total of 71 and 138 days exceeded this threshold for 2002 and 2005 respectively.

tion is that during the dry season, a single but sufficient rainfall amount is able to initiate growth in grazing lawns. The resulting green flush of young leaves can be of primary importance for herbivores during this period of limited food quality (Owen-Smith, Mason & Ogutu 2005; Valeix *et al.* 2008).

Surveying primary production at a monthly time-scale in the Serengeti, McNaughton (1985) reported that a minimum rainfall of 25 mm month⁻¹ was required for significant productivity of lawn grass areas. He also emphasized that the relevant time-scale between the two processes probably ranged from a few days to 1 week. When we convert our data to a monthly time-scale, we find that a minimum rainfall of 26 mm month⁻¹ is needed to reach the weekly threshold of 14 mm week⁻¹ at least once a month. This result closely matches McNaughton's observations. It indicates that the primary production of grazing lawns probably shows the same pattern of response to rainfall in both Hluhluwe and the Serengeti.

It is surprising that we did not find any significant effect of clipping frequency or clipping height on the relationship between rainfall and primary production. A large number of previous experiments on lawn grass species in the field (e.g. Hik, Sadul & Jefferies 1991; Green & Detling 2000) or in a glasshouse (e.g. McNaughton, Wallace & Coughenour 1983; Georgiadis *et al.* 1989) reported such effects. This result is probably explained by the predominant effect of rainfall, which overshadowed the effects of the clipping treatments we applied.

GRAZING LAWNS AND INTENSIVELY MANAGED GRASSLANDS

The use of grazing lawns by large herbivores raises the practical question of how sustainable foraging is under repeated grazing? This is a common question in intensively managed grasslands, which has led to the development of a large diversity of grazing systems for farm animals (Parsons 1988; Clark & Kanneganti 1998). 'Continuous variable stocking' systems

are a form of continuous stocking (see Spedding 1965; Parsons 1984) with a dynamics of grass production and consumption dynamics close to the one we observed in savanna grazing lawns. In grazing lawns, we showed that large herbivores maintained a sward of nearly constant standing biomass by quickly adjusting their grazing activity to the primary production. Similarly, in continuous variable stocking systems, farmers maintain a desired, typically short sward canopy height by frequently and carefully adjusting the stocking density of animals to primary production.

In continuous variable stocking systems, which are mainly used with lactating ewes and dairy cattle, maintaining a short sward canopy height does not constrain herbivores' intake levels to low values. Under continuous grazing, maintaining a short sward reduces the net photosynthetic rate of plants. But because of the rapid tissue turnover in grasses, it also increases the efficiency of forage use by improving the proportion of forage consumed to that which senesces and dies without having been eaten (see Parsons *et al.* 1983). When the balance between net photosynthesis, forage intake and tissues death is optimized, continuous variable stocking systems allow maximizing herbivores' intake levels by unit of grassland area (Ernst, Le Du & Carlier 1980; Grant *et al.* 1988; Parsons, Johnson & Harvey 1988; Pulido & Leaver 2003). For example, in temperate areas, when domestic herbivores are grazed on *Lolium perenne* L. swards, such maximum levels of intake are reached for a sward canopy height kept between 3 and 6 cm for sheep (Bircham & Hodgson 1983; Grant *et al.* 1983) and between 7 and 9 cm for dairy cattle (Ernst, Le Du & Carlier 1980). This highlights a key feature of short grasslands in that despite a low standing biomass, herbivores can maintain large levels of intake by using the sward more efficiently. This feature probably explains how grazing lawns support such high levels of intake, as long as rainfall is sufficient.

In both continuous variable stocking systems and grazing lawns, continuous grazing does not allow the build up of a consistent standing crop. As a result, instantaneous resource availability depends on the short-term rate of primary production. In natural systems, the diversity of the landscape allows herbi-

vores to use other areas when primary production ceases inside grazing lawns. But in intensively managed grasslands, the risk of pasture shortage constrains farmers to maintain areas devoted to forage conservation (i.e. buffer areas), or to conserve a stock of hay or silage (Mayne, Wright & Fisher 2000). The predominance of this farming practice emphasizes the general problem of resource unpredictability in continuously, intensively grazed areas.

Despite their dynamics being similar, grazing lawns and continuous variable stocking systems remain fundamentally different in their overall functioning. In intensively managed grasslands, farmers carefully adjust stocking densities as a function of their pasture management planning. As a result, they have control over sward canopy height. In grazing lawns, it is herbivores who adjust their own grazing activity as they are free to move in and out of these areas. Because grazing lawns are highly attractive resources, grazing activity increases in proportion to primary production. As a result, sward height remains short and herbivores have to decrease their consumption rates as soon as production slows down or ceases. Grazing lawn systems do not have the flexibility that farmers have in the range of sward height that can be maintained under intensively managed grassland systems. In some cases, it is possible that sward height of grazing lawns may approach a value that allows maximum levels of intake per unit area similar to that aimed for in intensively managed grasslands. Most of the time, however, sward height in lawns is probably lower than the ones that allow for these maxima.

Another important difference between the two systems lies in the nutritional role they play in the individual animals' diet. In intensively managed systems, the grazed forage forms the bulk of the animals' diet. To increase the production per animal, or to remedy any deficiencies in nutritional quality or quantity per animal, higher-quality feeds are usually provided in the form of supplements/concentrates. In contrast, although grazing lawns may represent the highest quality part of herbivores diet, the quantity consumed on a daily basis of this material may be limited because of the lawns' low standing biomass. Ultimately, these lawns may play a critical role in the herbivores nutrition. However, the bulk of the animal's diet, particularly over the seasonal time frame, is generally obtained in other, taller grassland or savanna areas that are of lower nutritional value.

Continuously stocked grazing systems and grazing lawns are similar with regard to their dynamics, but contrast with regard to their nutritional role in the herbivores' diet. This highlights the artificial nature of intensively managed grazing systems, which is not surprising as artificiality is part of the definition of intensive management (FGTC 1992).

Conclusion

By concentrating their grazing activity inside grazing lawns, large herbivores are able to maintain a short-cropped, highly nutritive grass. This can be of high nutritional interest, particularly in environments where the forage resource is often of poor nutritive value. Large herbivores also maintain high levels

of intake as short, repeated cropping maximizes the proportion of newly accumulated biomass consumed relative to that which senesces. However, maintaining a short-cropped sward means that instantaneous resource availability is a function of its short-term rate of growth. This is a general limitation on the use of short grass, not only in grazing lawns, but also in intensively, continuously stocked grazing systems in farms. In mesic to sub-arid environments, short-term primary production of lawn grass is driven by the weekly pattern of rainfall, a highly stochastic process. As a result, resource availability inside grazing lawns is highly unpredictable in time. It is therefore difficult for herbivores, in the elaboration of their foraging strategy, to develop a perfect knowledge of the resource available inside their habitat. Many models in foraging theory assume perfect knowledge of the environment (Stephens & Krebs 1986), but this assumption becomes quickly unreliable with grazing lawns. Grazing lawns are predictable in space, but unpredictable in time, and particularly vulnerable to changes in climatic conditions, such as changes in the frequency and intensity of droughts we face in the present context of climate change.

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