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Possible causes of decreasing migratory ungulate populations in an East African savannah after restrictions in their seasonal movements

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Abstract

In many areas in Africa, seasonal movements of migratory ungulates are restricted and their population numbers decline, for example in the Tarangire region, Tanzania. Here, agriculture restricts migration of ungulates to their wet season ranges. We investigated whether low forage quality or supply are possible causes of population decline of wildebeest and zebra when access to these wet season ranges is restricted and migratory herds have to reside in the dry season range year-round. We simulated grazing through a clipping experiment in the dry season range during the wet season. Clipping negatively affected forage supply and had a positive effect on forage quality by increasing proportions of live and leaf biomass as well as nutrient concentrations in the leaves. However, increase in forage quality in the dry season range due to grazing was not as such that requirements of wildebeest during the wet season, when females are lactating, could be met. We conclude that low forage quality in the dry season range during the wet season could cause the decrease in migratory ungulate populations in the Tarangire region. With this study, the necessity of protecting wet season ranges from expanding human activities to safeguard migratory systems is supported.

Key words: forage requirements, forage supply and quality, migratory system, simulated grazing, wildebeest

Résumé

Dans de nombreuses régions d'Afrique, les déplacements saisonniers des ongulés migrateurs sont entravés et leurs populations déclinent, comme par exemple dans la région de Tarangire, en Tanzanie. Ici, c'est l'agriculture qui limite la migration des ongulés vers les domaines qu'ils fréquentent en saison des pluies. Nous avons étudié si la mauvaise qualité ou la faible quantité du fourrage étaient des causes possibles du déclin des populations de gnous et de zèbres lorsque l'accès à leur domaine de saison des pluies est limité et que les troupeaux migrateurs doivent rester dans les domaines de saison sèche toute l'année. Nous avons simulé le pâturage en menant, en saison des pluies, une expérience de tonte dans l'aire fréquentée en saison sèche. Couper l'herbe avait un effet négatif sur l'apport de fourrage et avait un effet positif sur la qualité du fourrage parce que cela augmentait la proportion de biomasse vivante et de feuilles ainsi que la concentration de nutriments dans les feuilles. Cependant, augmenter par le pâturage la qualité du fourrage dans le domaine de saison sèche n'était pas suffisant pour satisfaire les besoins des gnous en saison des pluies, lorsque les femelles sont allaitantes. Nous concluons qu'en saison des pluies, la qualité médiocre du fourrage dans le domaine fréquenté en saison sèche pourrait causer la diminution des populations d'ongulés migrateurs dans la région de Tarangire. Cette étude conforte la nécessité de protéger les domaines fréquentés en saison des pluies contre l'expansion des activités humaines, afin de sauvegarder les systèmes migratoires.

Introduction

East African savannahs are known for large-scale seasonal migration of grazing ungulates (Fryxell & Sinclair, 1988; Wilmshurst *et al.*, 1999; Serneels & Lambin, 2001;

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Thirgood *et al.*, 2004). Generally, the annual cycle of migration involves movement between areas with permanent water availability, where the animals concentrate in the dry season, and surrounding grazing areas at the onset of the wet season. This movement has been explained by the higher nutritious quality of grass in wet season ranges compared to the dry season ranges (McNaughton, 1990; Mduma, Hilborn & Sinclair, 1999; Voeten & Prins, 1999; Boone, Thirgood & Hopcraft, 2006), but also other explanations have been put forward such as predation, insect avoidance, water quality and diseases (Boone *et al.*, 2006). During the dry season, most grasses are in a senescent phase of growth, and forage quality and supply are low in both wet and dry season ranges. In this paper, we ask the question of whether forage in the dry season range could be sufficient to sustain ungulate populations through a complete annual cycle.

Land use changes pose a challenge for migratory populations as rarely can both dry and wet season ranges be protected (Homewood *et al.*, 2001). It has been shown that degradation at either end of the migratory cycle can lead to a decline in migratory ungulates (Ottichilo, De Leeuw & Prins, 2001). An example of such a system is the Masai Ecosystem, Tanzania (Prins, 1987; Kahurananga & Silkiluwaska, 1997). Here, most migratory wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) congregate in Tarangire National Park during the dry season and a large proportion of these populations migrate to the Simanjiro plains, ±100 km east of Tarangire NP, at the onset of the wet season (Fig. 1). However, due to human settlement and agricultural activities, access to these unprotected plains is increasingly becoming restricted, and animals cannot stay in the wet season range due to lack of water during the dry season (Borner, 1985; TWCM, 1995; Bolger *et al.*, 2008). In the past two decades, this restriction coincided with a marked decline of the migratory populations, wildebeest in particular (Bolger *et al.*, 2008). We tested the hypothesis that forage in the dry season range during the wet season is of low quality and/or abundance. If so, this may contribute to the declining wildebeest population in the Masai Ecosystem.

Comparison of forage quality between wet and dry season ranges during the wet season show that forage quality in the wet season range meets herbivore nutritional requirements, while it does not in the dry season ranges (McNaughton, 1990; Murray, 1995; Voeten & Prins, 1999). However, most of these comparisons have been done during the wet season in which grazed wet season

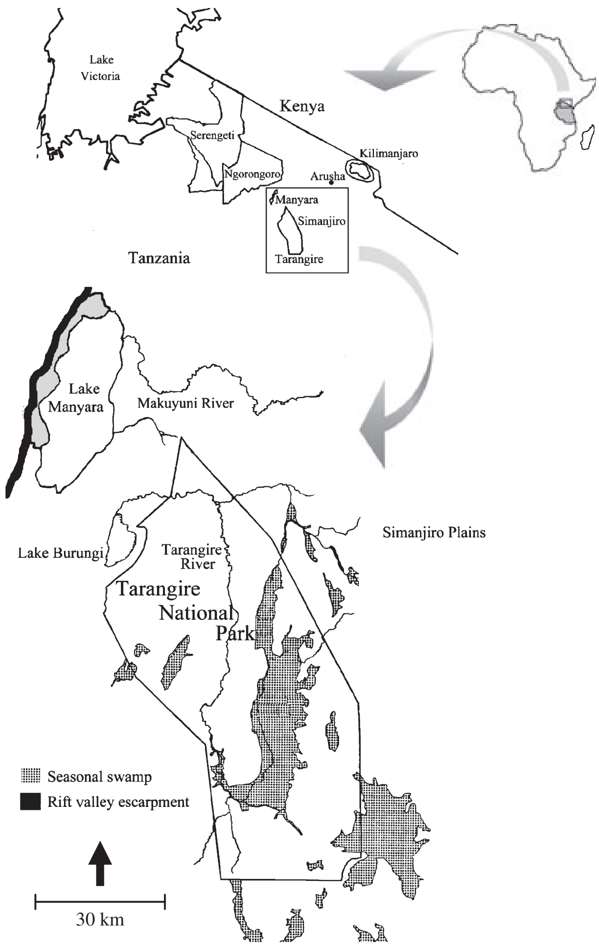

Fig 1 Tarangire National Park and surroundings. The Simanjiro plains, the main wet season range of the wildebeest and zebra is located at the east of the park

range herbage was compared with ungrazed dry season range herbage. When making these comparisons, the absence of herbivory in the dry season range during the wet season can be of importance since vegetation production and nutrient concentrations are not only determined by rainfall and soil nutrients (Bell, 1982; Le Houerou, Bingham & Skerbek, 1988), but also by herbivory itself. It has been shown that grazing during the growing season can keep the vegetation in a young, productive stage of growth, thus contributing to the maintenance of a high above-ground production of high quality (McNaughton, 1984; Oesterheld & McNaughton, 1991; Arsenault & Owen-Smith, 2002; Verweij *et al.*, 2006). To test this for the dry season range during the wet season, we simulated grazing through a clipping experiment with heavy and intermediate grazing pressure. We investigated effects of clipping on biomass production, composition of above-ground standing crop and mineral concentrations.

Methods

Study area

Data were collected in Tarangire NP (4° S, 36° E and 1200 m ASL), the dry season range of migratory herds of wildebeest and zebra. The park is located in the Masai Ecosystem, northern Tanzania and encompasses an area of ~2600 km^2 (Fig. 1). The Tarangire River runs through the park and is the main permanent dry season water source within the entire 35,000 km^2 Masai Ecosystem (Prins, 1987). In the park, vegetation ranges from floodplains along the river to open grasslands higher up the catena and wooded grasslands on the ridges (see Chuwa, 1996 for vegetation map). Soils are of lacustrine and alluvial origin underlain by preCambrian gneiss rock (Kahurananga & Silkiluwaska, 1997).

Average annual rainfall is 620 mm with high temporal and spatial variability. Most rain falls between December and May, while rainfall between June and November is very rare. Large migratory herds of wildebeest and zebra are present during the dry season and leave the park at the onset of the wet season. Other abundant herbivores in Tarangire NP are African elephant (*Loxodonta africana*), African buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), Coke's hartebeest (*Alcelaphus buselaphus cokii*), giraffe (*Giraffa camelopardalis*), Grant's gazelle (*Gazella granti*), oryx (*Oryx gazella*) and eland antelope (*Tragelaphus oryx*). These species, although more sedentary, also disperse over a larger area during the wet season and few animals remain in the park in this period.

Data collection

In Tarangire NP, we selected three locations along a topographical gradient: one on the floodplain in the river valley area, close to Tarangire River (River site), one on the open plains higher on the catena (Plains site), and one on a ridge slope (Ridge site). These sites represent the main soil/vegetation types on which the migratory ungulates congregate during the dry season (TWCM, 1995). The River site had light clay soils with high fertility and low drainage capacity. The vegetation is dominated by the grasses *Pogonarthria squarrosa* (Roem. & Schult.) Pilg, *Brachiaria decumbens* Stapf and *Urochloa mosambicensis* (Hack.) Dandy. The Plains site was situated on a brownish loam soil with medium fertility and medium drainage capacity. This site consisted of open grassland, dominated by *Chloris virgata* Swartz, *Dactyloctenium aegyptium* (L.) Willd, *Urochloa mosambicensis* and *Sporobolus ioclados* (Trin.) Nees. The Ridge site was located on red loamy sand soil with medium fertility and high drainage capacity. Here low tree cover was found, namely *Combretum apiculatum* Sond., *Balanites aegyptiaca* (L.) Del., *Adansonia digitata* L. and *Maerua triphylla* (Thunb.) Dur & Schinz. *Dactyloctenium aegyptium*, *Urochloa mosambicensis*, *Cynodon nlemfuensis* Vanderijst. and *Cenchrus ciliaris* L. dominated the grass layer.

Clipping experiment

The experiment started in January 1996 in the beginning of the wet season and lasted until September 1996, the middle of the dry season. With 943 mm of rain, the 1995–1996 rainy season was wetter than average. First rains came in the second half of December 1995 and the last rain fell at the end of May 1996. The Plains and Ridge sites were set up mid January and sampled nine times, while the River site was set up 2 weeks later and sampled eight times. In each site, five chain-link fence exclosures of 2.4 m by 1.2 m were set up with a minimum distance of at least 20 m to reduce pseudo-replication. Each exclosure was divided in three equal parts, each of them receiving a different clipping treatment. Heavy and intermediate grazing was simulated by clipping vegetation down to 3 and 15 cm height respectively every 3–4 weeks. The clipping height of the intermediate clipping treatment was based on average grass height found in the Simanjiro plains, the area that the Tarangire ungulates use during the wet season, while the height for heavy clipping represents intensive grazing (Belsky, 1986).

The control treatment was left unclipped because the exclosures were not big enough to harvest the unclipped treatment inside the exclosure throughout the growing season. Since most large ungulates were outside the park during most of the growing season, vegetation outside the exclosures could be considered as ungrazed and therefore biomass estimates of the unclipped treatments could be obtained by sampling 0.5 m × 1.0 m in matched plots outside the experimental exclosures. At the end of the growing season, all plots were clipped to 3 cm height. All clipped plant material was hand-sorted into green leaf, green stem and dead material, dried to a constant weight and weighed.

To describe the soil properties of the different sites, we collected five soil samples from each site in May 1996. Samples were collected with a metal pipe (∅ = 4.2 cm) at 0–10 cm depth. All soil samples were taken in duplicate and mixed to reduce spatial variability. Bulked samples were sieved through a 2-mm mesh to remove small stones and root material. Samples were dried to a constant weight and stored for chemical analysis.

Chemical analysis

The chemical analysis was done directly after the field work. Prior to chemical analysis, plant material and soil samples were digested using a modified Kjeldahl procedure with Selenium as a catalyst (Novozamsky *et al.*, 1983). Nitrogen (N) and phosphorus (P) concentrations in green leaves and soil material were analysed colorimetrically using a continuous-flow analyser (Skalar SA-4000; Skalar Analytical BV, Breda, The Netherlands). Calcium (Ca) and sodium (Na) concentrations were analysed with an Atomic Absorption Spectrophotometer (Varian Spectra AA-600; Varian, Houten, The Netherlands). Soil organic matter content was determined via combustion of soil samples at 550°C for 3 h. Soil pH was determined in the extraction residue from soil, using a 0.01 M $CaCl_2$ solution (Houba *et al.*, 1986).

Data analysis

Differences in soil mineral concentrations, soil organic matter and pH between sites were tested with a one-way ANOVA followed by Tukey HSD contrasts to compare means. The mineral concentrations were compared with rules-of-thumb from literature to estimate whether the grass can meet the requirements of the animals. To test for the differences in animal biomass production between the treatments and sites, we used a two-way ANOVA followed by Tukey HSD contrasts. Annual above-ground production for the unclipped treatment was calculated as the sum of the positive biomass increments between harvests (McNaughton, 1979). For the heavy and intermediate clipping treatments, annual production was calculated as the sum of the removed regrowth plus, for the intermediate clipping treatment, the biomass harvested at the end of the experiment.

To test for the differences in forage quality between the treatments and the sites over time, seasonal changes in the proportion of leaves, proportion of live biomass and nutrient concentrations in green leaves were analysed, using ANCOVA with clipping treatment as independent factor and harvest time as covariable. Leaf proportion was related to total live weight, while proportion of live biomass was related to total above-ground biomass. These proportions largely determine the selection of the grazers (Van Langevelde *et al.*, 2008). The above-ground biomass of the intermediate clipping treatment was calculated as the regrowth from each period plus an estimated value of the biomass between ground level and 15 cm. The latter was calculated by interpolating the biomass harvested at the end of the experiment for the intermediate treatment to the biomass at the beginning of the experiment. As we did not have a full factorial design (we did not replicated the sites), we subsequently tested the treatments pair-wise (intermediate-unclipped, heavy-unclipped and intermediate-heavy) per site. Prior to all statistical analyses, data were either log-transformed (biomass data) or arcsine-transformed (proportions and nutrient concentrations) to adjust for deviations of normality and to improve homogeneity of variance.

Results

The soil of the River site was more fertile than the Plains and Ridge sites with significantly higher concentrations of N, P, Ca and Na as well as higher organic matter content (Table 1). Only N concentration and soil pH did not differ significantly between the River site and the Plains site. In the beginning of the wet season, the vegetation recovered well from the clipping treatments leading to biomass values comparable to the unclipped vegetation (Fig. 2). However, from the middle of the wet season onwards, growth of the clipped treatments in all sites declined, and compared to the unclipped treatment eventually resulted

Table 1 Mean values of soil nutrients, soil organic matter and pH per site

Site	N (%)	P (%)	Ca (%)	Na (%)	Soil organic matter (%)	pH
River	0.16^{b}	0.11^{b}	0.63^{b}	0.10^{c}	10.61^{c}	6.16^{b}
Plains	0.10^{ab}	0.02^{a}	0.35^{a}	0.03^{b}	4.96^{b}	6.24^{b}
Ridge	0.06^{a}	0.04^{a}	0.35^{a}	0.05^{a}	3.04^{a}	5.86^{a}

Significant differences between sites are indicated by different letters within a column (one-way ANOVA between sites, $P < 0.001$ and Tukey-HSD contrasts).

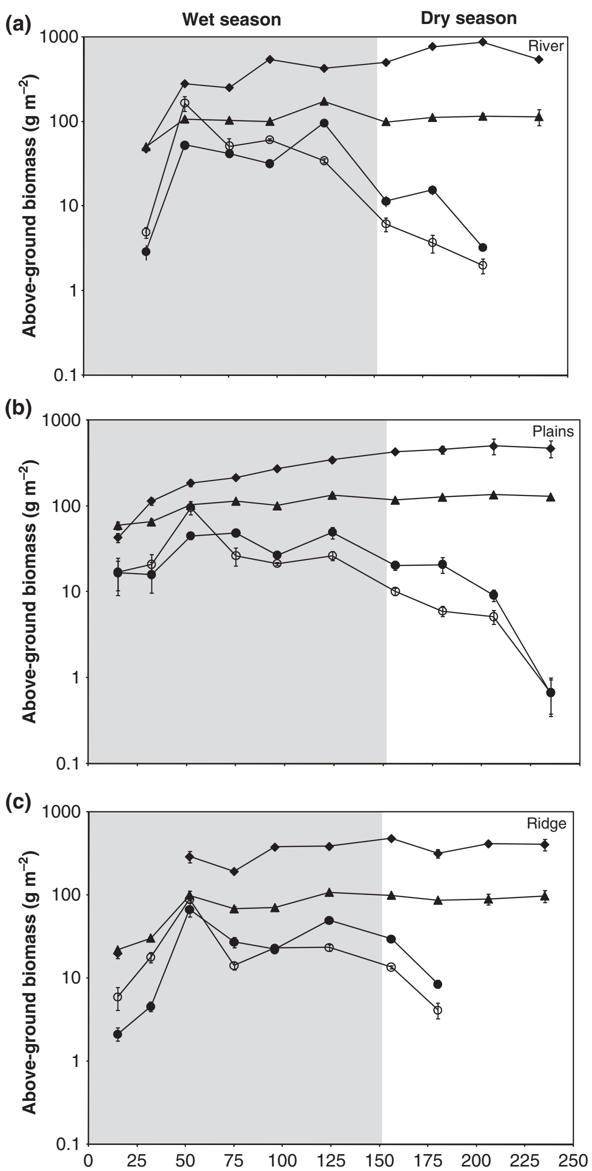

Fig 2 Average above-ground biomass (g m^{-2}, SE < 5% of the mean) for the unclipped (+) and intermediately clipped (▼) treatment, as well as regrowth of the intermediately clipped (●) and heavily clipped (○) treatments in the River, Plains and Ridge site in Tarangire National Park. Above-ground biomass for the intermediate clipping treatment is the sum of the regrowth plus the interpolated biomass under 15 cm. Day of harvest: Day 0 = 1-01-1996 and Day 235 = 22-08-1996

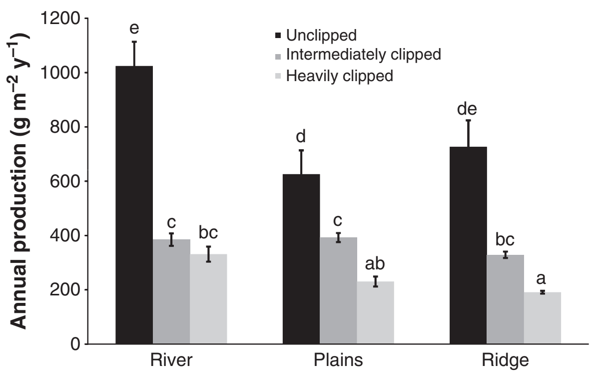

Fig 3 Mean annual production (g m^{-2} year^{-1}, ±SE) for the unclipped, intermediately and heavily clipped treatments in the River, Plains and Ridge sites in Tarangire National Park. Different letters denote significant differences (Tukey HSD, $P < 0.05$)

in a significantly lower annual production of above-ground biomass (Fig. 3). This effect was strongest in the River site which also had the highest unclipped annual production.

Composition of biomass

The proportion of live material was primarily determined by time in the season (date of harvest), and the effect of clipping became apparent into the dry season, keeping the proportion at a higher level as compared to the unclipped treatment (Fig. 4a–c and Table 2). The pair-wise comparisons between treatments per site showed that in most cases the effect of clipping increased during the experiment: the proportion of live material in the unclipped treatment decreased significantly more than in the two clipping treatments (see the significant interactions in Table 3). No significant differences were found between the intermediate and heavy clipping treatments.

The positive effect of clipping on leaf proportion (Fig. 4d–f) was already prominent in the wet season (see the explained variance per factor in Table 2). Generally, the River site showed lower leaf proportions than the Plains and Ridge site, probably due to a difference in grass species composition. Pair-wise comparisons per site between unclipped and clipped treatments showed a slight increase in leaf proportion in the clipped treatments and a decrease in the unclipped treatment during the course of the season (Table 3). Pair-wise comparisons revealed no significant differences between the heavy and intermediate clipping treatments at any of the sites.

Plant mineral concentrations

Generally clipping resulted in higher mineral concentrations in grass leaves (Fig. 5), but the effect varied among nutrients, sites and date of harvest. Most pair-wise com-

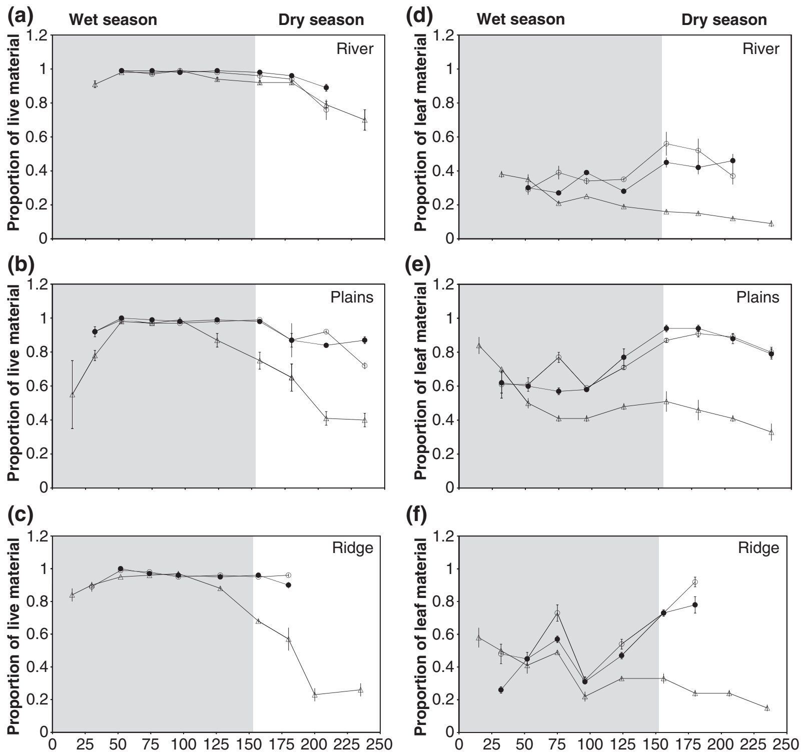

Fig 4 Mean proportions of live material (a–c) and leaves (d–f) for the unclipped (+), intermediately clipped (●) and heavily clipped (○) treatments in the vegetation in the River, Plains and Ridge site in Tarangire National Park. The proportion of live material was calculated as live biomass divided by live plus dead biomass. For the Ridge and River site, the proportion live in the clipped treatments at the end of the season could not be calculated because either no dead or live biomass was present. Day of harvest: as in Fig. 2

parisons between clipped and unclipped treatments showed that over time the clipped plots decreased less in N concentration than the unclipped treatments (Table 3). The differences between the intermediate and heavy clipping treatments were significant except for the River site.

Clipping also had a positive effect on P concentration in the leaves but the effect was less apparent than for N. Here too, the response differed between sites and was, depending on the site, affected by date of harvest or treatment (Fig. 5c–e and Table 2). Pair-wise comparisons between clipped and unclipped treatments showed that on the Plains and River sites, grass leaf P concentrations in clipped treatments showed the same trend in time as the unclipped treatments (Table 3). Only on the Ridge site, P levels increased more in the clipped treatments than in the unclipped treatments. No significant differences between the intermediate and heavy clipping treatments at any of the sites were found.

Ca concentrations were negatively affected by clipping but, just as for P, the response varied with site and date of harvest or by treatment (Fig. 5g–i and Table 2). On the Plains site, Ca levels increased during the season but clipping had no effect. On the River site, Ca levels also increased during the season but clipping resulted in a shallow increase. On the Ridge site, Ca levels were lower as a result of clipping but stayed constant over the year. Pair-wise comparisons between treatments showed no consistent pattern (Table 3).

Clipping and season had no clear effect on Na concentrations (Fig. 5j–l and Table 2), but between sites differences were large with ±15 times higher Na concentration in the River site than the Plains and Ridge. Moreover, pair-wise comparisons showed that, only in the River site, clipped treatments had higher Na concentration, and it decreased during the season (Table 3). None of the other comparisons differed significantly.

Consequences for herbivore forage quality

Mineral concentrations in the leaves were not sufficient over the season to meet the mineral requirements of wildebeest (Fig. 5). Mineral requirements for P, Ca and Na during lactation and pregnancy were taken from Murray (1995) who adjusted AFRC (1991) cattle requirements for wildebeest (see also Prins & Van Langevelde, 2008). The minimum N requirement for maintenance was set at 1.3% (Van Soest, 1994). In the wet season females are lactating and have high requirements, especially for P and Ca. The lactation period is ∼3–6 months, and in the beginning of

Table 2 The effect of clipping treatment (unclipped, intermediate or heavy) on the proportion of live material, the proportion of leaves and concentrations of N, P, Ca and Na in green leaves during the course of the season as tested in an ANCOVA with date of harvest as covariable

			Proportion		Grass leaf nutrient concentration			
Site	Factor	df	Live	Leaves	N	P	Ca	Na
River	Date (D)	1	47^{***}	2^{**}	52^{***}	15^{***}	50^{***}	31^{***}
	Treat (T)	2	5^{**}	51^{***}	18^{***}	6^{*}	18^{***}	12^{***}
	D × T	2	6^{***}	22^{***}	4^{**}	0^{ns}	10^{***}	1^{ns}
	r^2	5	58^{***}	74^{***}	74^{***}	21^{***}	78^{***}	44^{***}
Plains	Date (D)	1	35^{***}	4^{***}	32^{***}	0^{ns}	37^{***}	0^{ns}
	Treat (T)	2	19^{***}	60^{***}	29^{***}	19^{***}	0^{ns}	3^{ns}
	D × T	2	26^{***}	10^{***}	6^{***}	2^{ns}	1^{ns}	6^{ns}
	r^2	5	79^{***}	73^{***}	67^{***}	21^{***}	39^{***}	9^{ns}
Ridge	Date (D)	1	49^{***}	0^{ns}	51^{***}	6^{**}	0^{ns}	0^{ns}
	Treat (T)	2	13^{***}	38^{***}	17^{***}	30^{***}	12^{**}	7^{ns}
	D × T	2	25^{***}	29^{***}	1^{ns}	4^{*}	2^{ns}	4^{ns}
	r^2	5	87^{***}	67^{***}	68^{***}	40^{***}	14^{**}	11^{ns}

Values indicate the percentage of variance explained per factor, summing up to the variance explained by the model (r^2). The explained variance per factor was calculated as the sum of squares (SS) per factor divided by the SS of the corrected total. The significance levels refer to the *F*-test of the ANCOVA (ns = not significant, $^*P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$).

the dry season the calves are weaned and mineral requirements drop to maintenance and pregnancy levels. N, P and Na requirements of zebra are comparable to wildebeest's (Duncan, 1990), while Ca requirements are slightly higher.

Clipping increased N concentration so that these were above maintenance levels for a longer period of time (Fig. 5a–c). P levels were, however, continuously too low in the wet season when females are lactating (Fig. 5d–f). Ca concentrations were above lactation and pregnancy requirements throughout the wet and dry season (Fig. 5g–i). Na levels in the grasses in the soils found in the Plains and Ridge sites are too low for lactating and pregnant females, but high enough in the soils of the River site (Fig. 5j–l).

Discussion

As migratory routes between seasonal ranges for Masai Ecosystem herbivores become nonpassable due to development, these populations tend to remain in Tarangire NP year-round, which has had apparently dire consequences for population numbers (Bolger *et al.*, 2008). Although grazing may enhance forage supply, our study shows that, for all three soil types investigated, clipping adversely affected grass biomass, with significantly lower annual production in both clipped treatments compared to the unclipped treatment. Other studies have, however,

Table 3 Pair-wise comparisons between treatments (unclipped, intermediate and heavy) per site for the proportion of live material, the proportion of leaves and concentrations of N, P, Ca and Na in green leaves during the course of the season as tested in an ANCOVA with date of harvest as covariable

		Proportion		Grass leaf nutrient concentration			
Site	Factor	Live	Leaves	N	P	Ca	Na
Unclipped-heavy							
River	*Date (D)*	***	***	***	***	***	***
	Treat (T)	ns	***	***	*	***	***
	D × T	*	***	**	ns	***	ns
Plains	*Date (D)*	***	ns	***	ns	***	ns
	Treat (T)	***	***	***	***	ns	ns
	D × T	***	***	***	ns	ns	ns
Ridge	*Date (D)*	***	***	***	ns	ns	ns
	Treat (T)	***	***	***	***	**	ns
	D × T	**	***	ns	*	ns	ns
Unclipped-intermediate							
River	*Date (D)*	***	***	***	***	***	***
	Treat (T)	***	***	***	*	***	*
	D × T	***	***	**	ns	***	ns
Plains	*Date (D)*	***	*	***	ns	***	ns
	Treat (T)	***	***	***	***	ns	ns
	D × T	***	***	**	ns	ns	ns
Ridge	*Date (D)*	***	*	***	*	ns	ns
	Treat (T)	***	***	***	***	**	ns
	D × T	***	***	ns	*	ns	ns
Intermediate-heavy							
River	*Date (D)*	***	***	***	**	***	***
	Treat (T)	ns	ns	ns	ns	ns	*
	D × T	*	ns	ns	ns	ns	ns
Plains	*Date (D)*	***	***	***	ns	***	ns
	Treat (T)	ns	ns	**	ns	ns	ns
	D × T	ns	ns	ns	ns	ns	ns
Ridge	*Date (D)*	ns	**	***	***	ns	ns
	Treat (T)	ns	ns	*	ns	ns	ns
	D × T	**	ns	ns	ns	ns	ns

For reason of clarity only significance levels are given. These levels refer to the *F*-test of the ANCOVA (ns = not significant, $^*P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$).

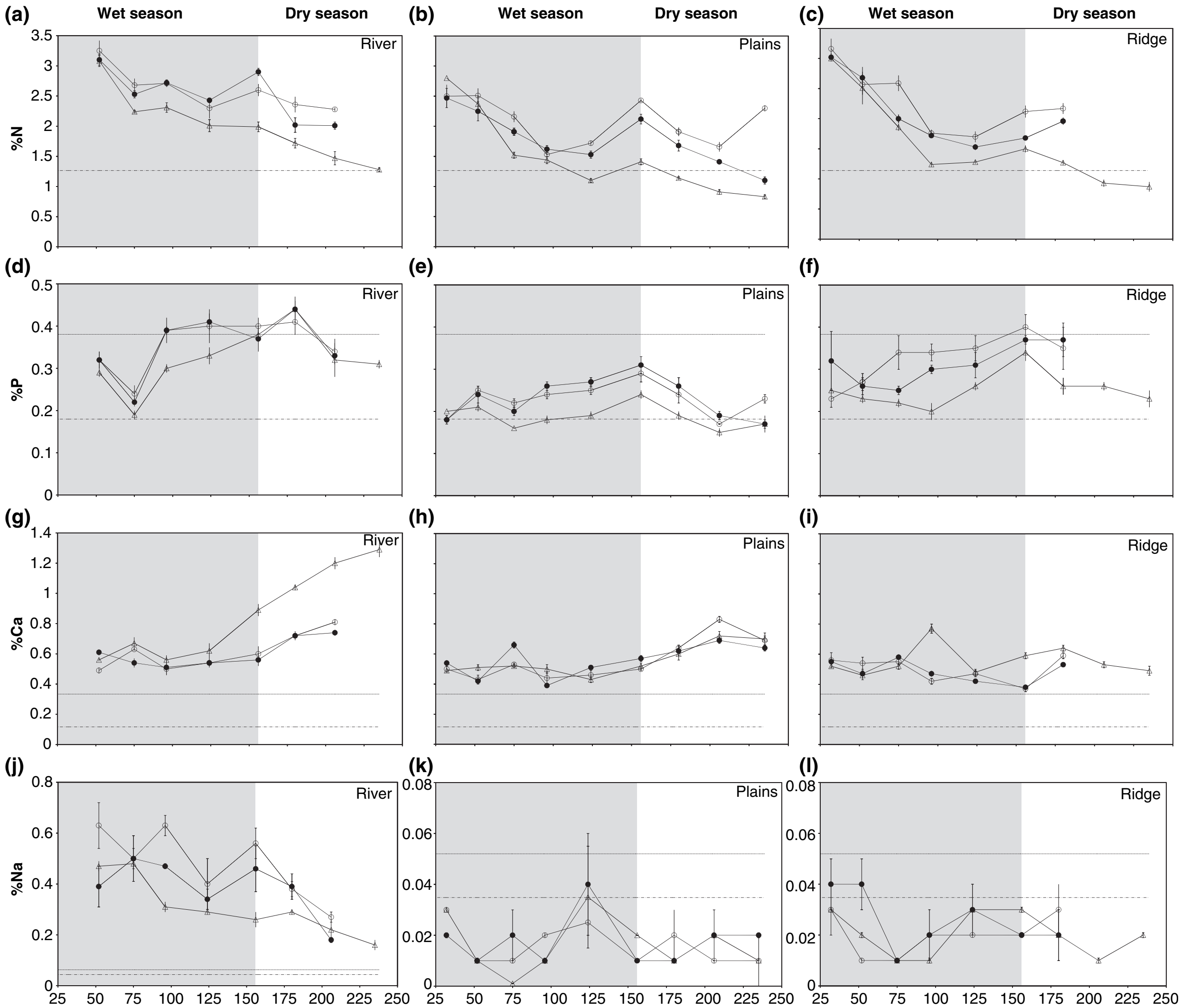

Fig 5 Concentration of N (a–c), P (d–f), Ca (g–i) and Na (j–l) in green leaves in the River, Plains and Ridge sites, respectively in Tarangire National Park for unclipped (+), intermediately (●) and heavily clipped (○) treatments. No data are available for clipped treatments in the Ridge and River site at the end of the season due to lack of material. Note that the %Na-axis for the River site has a different scaling than for the Plains and Ridge site. Minimum N requirement for maintenance (— - —) as well as minimum requirements of P, Ca and Na during pregnancy (— - —) and lactation (- - - -) is indicated. Day of harvest: as in Fig. 2

shown that in semi-arid systems grazed vegetation can compensate for the amount of material grazed and in some situations can even produce more than ungrazed vegetation (McNaughton, 1979; Oesterheld & McNaughton, 1991). The lack of compensatory growth in our study may be the result of an exceptionally wet year in which the experiment was performed: water, the main limiting growth factor in these semi-arid savannahs, was ample, hence reducing the relative importance of the positive effect that biomass removal can have on loss of water by reducing transpiring leaf area (McNaughton, 1979). It is unlikely that limited soil nutrient availability explains this lack of compensatory growth as we found that the most nutrient-rich site, the River site, showed the least compensation after clipping compared to the other sites.

On the other hand, we found an increase in forage quality, such as the proportion of leaves and live material that were higher in the clipped vegetation compared to the unclipped vegetation. Additionally, the mineral concentrations of leaf material were higher in the clipped treatments with particularly higher concentrations of N and to a lesser extent also P. This positive effect of clipping on grass leaf N and P concentrations can be partly explained by a reduced dilution due to a lower increment of standing plant material in the clipped treatment compared to the unclipped treatment (Milchunas *et al.*, 1995). The younger age of leaves in the clipped treatments may also explain the higher tissue nutrient concentrations since nutrient concentrations decrease during aging (McNaughton, 1979; Hassall, Riddington & Helden, 2001).

Now the question is if this increase in quality is sufficient to meet the requirements of the migratory herbivores? Our study shows that, even though N concentration can be kept above maintenance requirements of wildebeest for a longer period of time through grazing, forage quality will eventually fall below the critical levels. In most semi-arid systems, N concentration in the vegetation is well below maintenance levels during a great deal of the dry season (Boutton, Tieszen & Imbamba, 1988; Prins, 1996), and most animals will use their reserves which were built up during the wet season. So, the positive effect of grazing on N levels in the vegetation will delay the use of these reserves, and hence can be advantageous for the grazing animals, particularly when the dry season is prolonged.

Although P concentration was also enhanced through clipping, the increase was not sufficient to reach levels required by lactating wildebeest females during the wet season. This was again found in the 1996–1997 wet season: P concentration in leaves in the areas where animals were grazing after their return was on average 0.32% ($n = 15$, green leaves only, unpublished data V. Galanti) and thus also below lactation requirements. Short periods of limitation may be overcome by release of P stored in bones (Wallis de Vries, 1996), but quantitative information on this is not yet available. Also Na concentration, which was not consistently enhanced by clipping, remained below requirement levels, except for the River site where concentrations in all treatments were exceptionally high. Although Ca concentration tended to be reduced through clipping, rather than increased, concentrations were above lactation requirements in all treatments and sites, and therefore would not appear to be a problem for year-round presence of the migratory herds. Due to low P and Na concentrations in the leaves, however, exclusive foraging on these grasses in the dry season range during the lactation period may affect herbivore reproduction and survival of their young. Moreover, since our interpretation of forage quality was based on green leaf material only, and herbivore diet also contains stem and dead material, the mineral intake will be even less and requirements will be even more difficult to meet than suggested above. If a mineral (Ca, K, Na) is available, then there is little need for these to be of high value in the forage. Such additional supplies of minerals by drinking (river)water or soil consumption (Kreulen & Jager, 1984) may be important when nutrient concentrations in the vegetation are too low (McNaughton, 1988), but quantitative data on the importance of these resources are lacking (Gereta *et al.*, 2004).

Although grazing positively affects forage quality, we conclude that not only forage supply but also quality in the dry season range during the wet season could cause the decrease in migratory ungulate populations of Tarangire region. These populations are more and more confined to their dry season range year-round, and we hypothesize that the resulting forage quality in Tarangire NP cannot sustain large ungulate populations. This supports recent findings of decline in migratory ungulates (Kahurananga & Silkiluwaska, 1997; Homewood *et al.*, 2001; Serneels & Lambin, 2001; Bolger *et al.*, 2008). Moreover, as result of continuous high grazing pressure in the dry season range year-round, a change in forage species composition to less palatable species can be expected (Coppock *et al.*, 1983), even an increase of woody vegetation (Roques, O'Connor & Watkinson, 2001). This might reinforce our conclusion that forage quality in the dry season range during the wet season is not sufficiently high to support large migratory ungulate populations. Although our conclusions are based on the short-term effects of simulated grazing during 1 year, and do not include such possible long-term changes in plant species composition, the present study supports the claim that protection of migration routes and wet season grazing areas is essential to safeguard migratory ungulate populations.

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