Aboveground Net Primary Productivity in Grazed and Ungrazed pastures: Grazing Optimisation Hypothesis or Local Extinction of Vegetation Species

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Abstract
The controversy that has surrounded herbivory studies in the last few decades prompted our investigation to establish the extent to which herbivore optimisation hypothesis or compensatory growth evidence is real. We used the traditional movable cage method to collect primary productivity data on herbage, functional groups and key individual grass species in various controlled large herbivore treatments in an east African savanna. The herbivore treatments in triplicate blocks included cattle, wild herbivores with and without mega herbivores and combinations of cattle and wild herbivores also with and without mega herbivores. The findings revealed that at herbage level, most grazed treatments (four out of five) had higher productivity than the ungrazed control and three showed grazing optimisation curve at sixth polynomial degree between monthly productivity and grazing intensity (1-g/ng). At functional group level forbs productivity was higher in the ungrazed control than in any of the grazed treatments while at individual grass species level *Themeda triandra* productivity was higher in all grazed treatments than in ungrazed control. We conclude against presence of herbivore optimisation hypothesis at herbage, functional group and species level because of lack of attributable grazing effect in grazed treatments that matches complex ecological effects in the ungrazed treatment.

Key words: *grazed treatments, ungrazed control, movable cage method, wild herbivores, cattle, primary productivity, grazing optimisation curve*

Introduction

One of the most persistent controversies in herbivory studies concerns the “grazing optimisation hypothesis”. Its proponents (McNaughton, 1979; Hilbert *et al.* 1981, Dyer *et al.* 1986) believe and have reported evidence that certain levels of herbivory on plants causes compensatory growth. They insist that compensatory growth causes plant productivity to initially increase with increasing grazing intensity, reach maximum at moderate and then decline at high grazing intensity. This in turn results in measurable incremental plant biomass (net primary production) in moderately grazed plants that is greater than ungrazed controls.

The evidence supporting this grassland character has supported by experimental studies (McNaughton 1979; 1983; Cargill and Jefferies 1984; Georgiadis *et al.* 1989; Hik and Jefferies 1990), and models (Hilbert *et al.* 1981; Dyer *et al.* 1986; de Mozancourt *et al.* 1998; Leriche *et al.* 2001)

Models of herbivore utilisation have also supported the hypothesis when it affects the rate of recycles of limiting nutrient (Dyer *et al.* 1986), affects relative growth rate of plants during certain period of growth (Hilbert *et al.* 1981), results in loss of limiting nutrient (de Mozacourt *et al.* 1998), or causes restriction of available resources required by growing plants (Leriche *et al.* 2001). Some authors (Georgiadis *et al.* 1989) have sought to determine the underlying ecological conditions within which over-compensation is feasible.

The opponents of over-compensation (Belsky 1986; 1987; McNaughton 1986; Belsky *et al.* 1993) argue that the evidence is weak to non-existatn, and is of little significance to terrestrial ecologists and grassland managers in any case. They point out that some grassland managers have used reports of over-compensation to increase their stocking rates to their own destruction; by causing adverse consequences on the integrity of grasslands.

Experimental and modelling studies have not tested the herbivore optimisation hypothesis in grasslands where different groups of large herbivores such as cattle, wild herbivores or their combinations concurrently utilise different pastures within the same ecosystem. We further note that obscure explanation has been provided regarding the functionality and application of the hypothesis beyond herbage aboveground net primary productivity. In particular, we investigate the relevance of the optimisation hypothesis when ANPP is partitioned to specific functional groups such as perennial grasses, annual grasses, and forbs, or among grass species within an community. We ask whether there are situations when compensatory growth can occur for ANPP of overall herbage, as well as for functional groups or individual grass species. Investigations regarding compensatory growth and herbivore optimisation hypothesis need to be carried out to appropriately respond to the needs of grassland managers as well as academic scientists.

Material and methods

Site description

The study was conducted at the Mpala Research Centre located 45 kilometres northwest of Nanyuki town in Laikipia district, Rift Valley province, Kenya. The centre is situated on longitude 36° 54' 0"E and latitude 0° 17' 24"N in the Ewaso Nyiro North ecosystem at an average altitude of 1800m above sea level. The site is a black cotton ecosystem whose overstorey vegetation is dominated by *Acacia drepanolobium* (Young *et al.* 1998).

Treatments and experimental layout

The experiment was organized in a stratified block design with six treatments namely cattle (C), wild herbivores with [MW] and without [W] mega herbivores, combined cattle and wild herbivores with [MWC] and without [WC] mega herbivores and, ungrazed control (O), which excluded all large herbivores in the pastures. Mega-herbivores (M) in this study refer to elephants (*Loxodonta africana*) and giraffes (*Giraffa camelopardalis*). Wild herbivores (W) refer to a group of large mammalian wild herbivores smaller than the mega herbivores including zebras (*Equus burchelli* and *Equus grevyi*), buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), Beisa oryx (*Oryx gazella*), hartebeest (*Alcelaphus bucelaphus*) and Grant's gazelle (*Gazella granti*). The experiment used wildlife and mega herbivore fences while cattle barriers in pastures dedicated for wild herbivores alone were visual (for details, see Young *et al.* 1998). The study evaluated herbaceous layer ANPP compensation after eight years of treatment application in a black-cotton-soil savanna ecosystem.

Each treatment was replicated three times along North-South gradient for a total of eighteen pastures of 4 hectares each. These treatments represented diverse land use and management alternatives practiced in most arid and semi arid lands in Kenya and elsewhere in the African continent.

Replicates, sample size and productivity calculations

Aboveground net primary productivity was sampled four times over an effective period of 133 days in the growing seasons between August 2002 and May 2003, using movable cage method. Each cage measuring 1mX1mX1m had metal bar frames covered with chicken-wire mesh. Cages were set randomly in treatment pastures as recommended by Klingman *et al.* (1943) and moved in pasture plots as described by McNaughton *et al.* (1996). Each 4 ha pasture plot was divided into different zones each with a cage. Randomisation of sampling stations was done in each of these zones for all the sampling dates for each treatment plot at the beginning of the study period. At each sampling date, five 1m^2 cage plots and un-caged counterparts were selected randomly in each of the 4 ha treatment pasture. All the herbage biomass in each of these plots was clipped to the ground level. The un-caged plot (reference) plot was clipped immediately at the time caged one was being set up. The caged plot stayed in the field for an average number of days of 21.2±0.9, 36.3±1.6, 26.7±0.4 and 46.0±0.0 for the first, second, third and forth sampling dates respectively. After each sampling date, cages were randomly moved to different sampling station but within the same zone in the 4 ha treatment plot. Paring of caged and uncaged plot was done at each sampling date. Increments in production were calculated by subtracting herbage biomass in the un-caged plot from the herbage biomass in the caged plot. Production increments from all five sampling points within 4 ha treatment pasture plot were averaged irrespective of whether negative or positive (McNaughton *et al.* 1996). This mean represented increment production for the sampling date for the treatment pasture. Mean Incremental production from various sampling dates were summed together to form aboveground net primary production (ANPP) over the effective study period. Effective study period in the growing season refers to the mean total number of days in which movable cages remained in the field. The mean ANPP for each treatment was obtained by averaging ANPP from the three different blocks (North, Central and South). Mean ANPP for each grazed treatment was compared to that of the (ungrazed) control and observed whether above or below those of the control.

Sampling

Each grass species present in the plot was clipped and packaged in its own labelled paper bag. Paper bag details included grass species, herbivore treatment, sampling station location or co-ordinates, plot status (either reference or caged) and date. The other harvested functional groups were placed into specific paper bag (e.g. all forbs or all collected litter were put into own separate paper bags at the time of harvesting). These were dried to a constant weight at internal (within the bag) temperatures ranging between 50^{o}C to 80^{o}C in a forced draught oven for 24 hours before weighing (8 hours drying per day for three consecutive days).

Results

The mean herbage ANPP in W, C, MWC, and WC treatments exceeded those of control treatment by 153.6 gm^{-2}, 72.7 gm^{-2}, 54.5 gm^{-2} and 28.6 gm^{-2} respectively while the herbage ANPP of MW treatment was less than that of control treatment by 83.6 gm^{-2}. Monthly herbage ANPP and grazing intensity (1-g/ng) as applied in McNaughton (1979) also showed diversity of fitted curves. Most grazed treatments presented linear relationships for fitted polynomial curves from 0 to 5th degree on monthly productivity and grazing intensity as applied in McNaughton (1979). At sixth degree polynomial most grazed treatments exhibited herbivore optimisation curve (Figures 1-3) but not all see Figure 5 and 6. Surprisingly, even the non-grazed treatment presented a herbivore optimisation curve (Figure 4). This casted doubt whether grazing optimisation curve resulting from grazing intensity (1-n/ng) in McNaughton 1979 is practical.

Table 1 presents mean ANPP for functional groups after subtracting ANPP measured in respective control treatment. The results show that at functional group level perennial grasses consistently maintained ANPP above the control values in W, WC, MWC and C while MW had lower productivity of perennial grasses than the ungrazed control. However, ungrazed control maintained higher forbs productivity than any of the grazed treatments. Annual grasses productivity also appeared to be lower than the control in all grazed treatments except in WC. Sedges productivity was lower in C and MW than the control but higher in all other grazed treatments.

Table 2 below presents mean ANPP for five key grasses. The results show that *Themeda triandra* maintained higher productivity above the ungrazed controls. Relative to control productivity, *Brachiaria lachnantha* and *Pennisetum mezianum* had higher productivity in all grazed treatments except in MW and MWC respectively. *Pennisetum stramineum* maintained productivity above the control in WC, MWC and W but not in C and MW. Of all the grazed treatments, *Lintonia nutans* maintained its productivity above the ungrazed control in WC only.

Table 1. Mean ANPP for functional groups in grazed treatments after subtracting respective ANPP of the ungrazed control

Treatment	Perennial grasses	Forbs	Annual grasses	Sedges
C	76.1	-53.7	-0.6	-0.9
WC	99.2	-57.8	0.6	1.7
MWC	89.4	-29.7	-0.9	1.5
W	230.6	-92.2	-0.3	0.2
MW	-11.8	-46.1	-0.3	-2.3
O	0.0	0.0	0.0	0.0

Table 2. Mean ANPP for individual dominant grasses in grazed treatments after subtracting respective ANPP of the ungrazed control

Treatment	*Themeda triandra*	*Brachiaria* Lachnantha	*Pennisetum mezianum*	*Pennisetum stramineum*	*Lintonia Nutans*
C	42.7	86.2	89.6	-19.9	-5.2
WC	31.4	21.1	54.9	16.9	3.2
MWC	100.4	34.2	-2.8	95.9	-20.6
W	151.7	124.6	156.4	60.4	-49.1
MW	32.0	-12.3	111.7	-23.0	-4.3
O	0.0	0.0	0.0	0.0	0.0

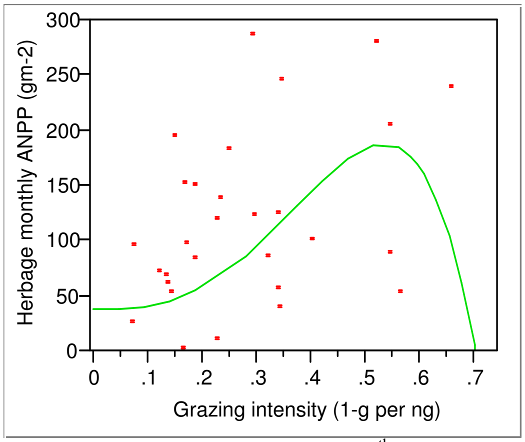

Figure 1. Cattle treatment (C) fitted 6th degree polynomial

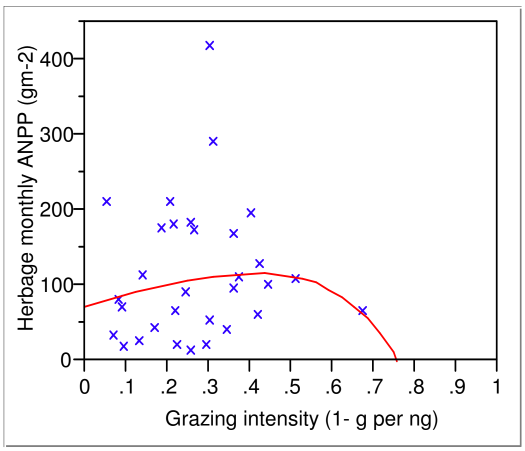

Figure 3. Wild herbivores, cattle with mega herbivores (MWC) fitted 6th degree polynomial

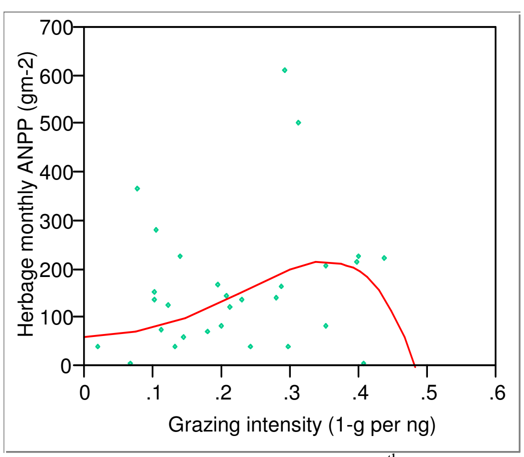

Figure 2. Wild herbivores (W) fitted 6th degree polynomial

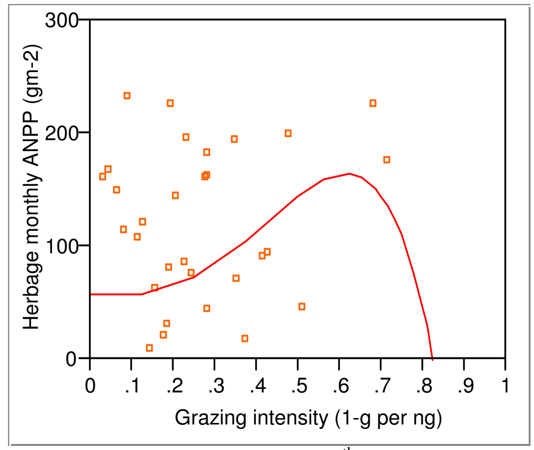

Figure 4. Non-grazed (O) fitted 6th degree polynomial

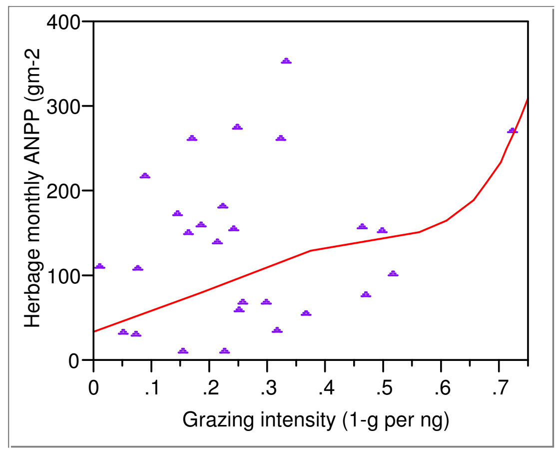

Figure 5. Wild herbivores and cattle without mega herbivores (WC) fitted 6th degree polynomial

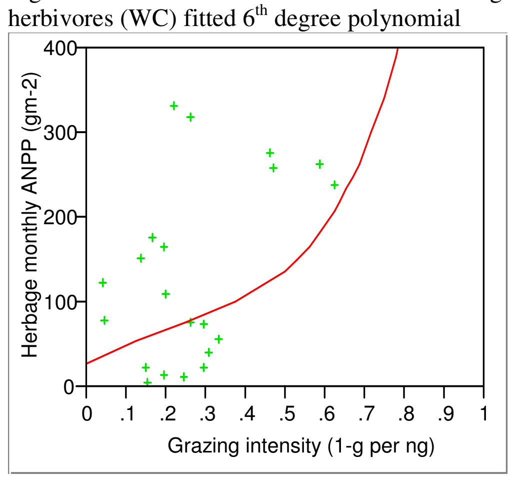

Figure 6. Wild herbivores plus mega herbivores (MW) fitted 6th degree polynomial

Discussion

Herbage, functional groups and individual grass species revealed differing dimensions when net primary productivity of grazed treatment is first corrected with that of ungrazed control.

Herbage productivity

We found evidence that herbage productivity in all grazed treatments except in MW were above those of the ungrazed control. It is apparent that presence of different kinds of large herbivores in pastures caused herbage productivity to range between 153.6 gm^{-2} to 28.6 gm^{-2} over and above the ungrazed control. This wide range could conveniently be attributed to the extent to which herbage was utilised, for example W though had highest productivity, was utilised the least by large herbivores compared to WC (Otieno, 2004 and Otieno et al. in prep). Also herbage productivity in MW was below that of the ungrazed control despite maintaining second highest mean herbage standing biomass (Otieno *et al.* in prep). However, many grazed treatments provided higher productivity than the ungrazed control, and revealed a sign of optimisation curve at fitted sixth degree polynomials (Figures 1-3), we could not attribute these as evidence for compensatory growth or confirmation of herbivore optimisation hypothesis. This is because herbage is an amorphous parameter that summarises all the components of grassland pasture. We therefore advanced our investigation to functional group level.

Functional groups

Productivity of perennial grasses in all grazed treatments except MW were over and above the ungrazed control, however forbs productivity in all grazed treatments was below those of the control. W productivity for perennial grasses was maximum when that of forbs was most minimum. Here we observe that perennial grasses show evidence for compensatory growth at the same time forbs disapprove it by revealing strong anti herbivore optimisation hypothesis evidence. Further other functional groups such as annual grasses and sedges reveal mixed evidence in different grazed treatments. These again do not provide sufficient evidence for adoption of optimisation hypothesis or rejection since the grassland functionality need to be looked at holistically. The best we can derive here is that most grazed pastures could overcompensate productivity for perennial grasses and all could under-compensate productivity of forbs when those of annual grasses and sedges contribute loud noise in the data. Why? The extent to which managers can apply this finding in their management plans is limited, while the extent to which scientists can use it to advance or redirect further research to investigate compensatory growth is also limiting. Since all forbs did under-compensate we did not pursue them in analysis instead we pursued the line of grasses to unveil details regarding the evidence.

Grass species

Most key grasses; T. *triandra*, B. *lachnantha*, P. *mezianum*, and P. *stramineum* provided results indicating higher productivity in grazed than the ungrazed controls. L. nutans appeared to have higher productivity in the ungrazed control than in most grazed treatments however this does help much in explaining the application of herbivore optimisation hypothesis. It can only add to the controversy had we not holistically analysed the problem. However, we used *Themeda triandra;* a well researched grass in east and southern Africa to help in explaining the mystery behind herbivore optimisation hypothesis.

We observed that *Themeda triandra* productivity in all the grazed treatments were over and above those of the ungrazed control. This would have otherwise been viewed as over compensation but we noted that the vigour and abundance of *Themeda triandra* in the ungrazed treatment reduced significantly thereby affecting their productivity. Belsky (1992) made similar observation and noted that functionality of *Themeda triandra* declined tremendously in exclosed than in grazed pastures. O'Connor (1991) classified *Themeda triandra* among extinction prone perennial grass common in subclimax or climax community. Elsewhere, Mott *et al.* (1985) estimated the longevity of this grass to be approximately 10 years because their seed lasts few years after which the grass could result to local extinction. This local extinction could have caused their productivity to be less in the ungrazed pastures and this could lead to misinterpretation of data to be viewed as over-compensation resulting from grazing.

Conclusion

We note that productivity in grazed and ungrazed pastures may differ at any level of observation-herbage, functional group or species. We also note that presence of large herbivores may promote vigour of individual plants by a number of ways other than an act of grazing or browsing; for example by encouraging seed dispersal and consequent recruitment of new seedlings. However, given the evidence revealed by our study we could not find concrete evidence to attribute higher productivity in pastures with presence of large herbivores to confirm herbivore optimisation hypothesis. This is because a number of factors especially that of local extinction of individual plant species appears to be in control in ungrazed pastures than in grazed ones. We therefore find it is simplistic to compare grazed and ungrazed pastures in terms productivity of combined herbage, forbs or grasses because there are fundamental ecological differences, which influencing them differently. For instance the balance of grasses and forbs biomass in grazed and ungrazed treatments differ (Otieno et al. in prep). We finally conclude that conducting research with contemporary methods such as movable cage methods to investigate evidence for compensatory growth or herbivore optimisation hypothesis as has been done previously is too simplistic to provide a viable direction for research in this area.

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