A test of two mechanisms proposed to optimize grassland aboveground primary productivity in response to grazing

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Abstract

Aims

Mesic grasslands have a long evolutionary history of grazing by large herbivores and as a consequence, grassland species have numerous adaptations allowing them to respond favourably to grazing. Although empirical evidence has been equivocal, theory predicts that such adaptations combined with alterations in resources can lead to grazing-induced overcompensation in aboveground net primary production (ANPP; grazed ANPP > ungrazed ANPP) under certain conditions. We tested two specific predictions from theory. First, overcompensation is more likely to occur in annually burned grasslands because limiting nutrients that would be lost with frequent fires are recycled through grazers and stimulate ANPP. Second, overcompensation of biomass lost to grazers is more likely to occur in unburned sites where grazing has the greatest effect on increasing light availability through alterations in canopy structure.

Methods

We tested these nutrient versus light-based predictions in grazed grasslands that had been annually burned or protected from fire for >20 years. We assessed responses in ANPP to grazing by large ungulates using both permanent and moveable grazing exclosures (252 exclosures from which biomass was harvested from 3192 quadrats) in a 2-year study. Study sites were located at the Konza Prairie Biological Station (KPBS) in North America and at Kruger National Park (KNP) in South Africa. At KPBS, sites were grazed by North American bison whereas in KNP sites were grazed either by a diverse suite of herbivores (e.g. blue wildebeest, Burchell's zebra, African buffalo) or by a single large ungulate (African buffalo).

Important Findings

We found no evidence for overcompensation in either burned or unburned sites, regardless of grazer type. Thus, there was no support for either mechanism leading to overcompensation. Instead, complete compensation of total biomass lost to grazers was the most common response characterizing grazing–ANPP relationships with, in some cases, undercompensation of grass ANPP being offset by increased ANPP of forbs likely due to competitive release. The capability of these very different grass-dominated systems to maintain ANPP while being grazed has important implications for energy flow, ecosystem function and the trophic dynamics of grasslands.

Keywords: aboveground net primary production • fire • forbs • herbivores • savanna

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INTRODUCTION

Grasslands, with their strong co-evolutionary history with large grazers (Coughenour 1985; Stebbins 1981), can be surprisingly variable with regard to the nature of plant–herbivore interactions. Although herbivory has traditionally been viewed as a negative interaction from the plant's perspective, both theoretical and empirical studies in grasslands suggest that individual plants, as well as primary productivity at the ecosystem scale, may respond in a neutral or even a positive manner to grazing (Frank *et al.* 1998; McNaughton 1979). A positive aboveground net primary production (ANPP) response to grazing under certain conditions is predicted by the grazing optimization hypothesis (Hilbert *et al.* 1981) and has been termed overcompensation. Overcompensation has garnered much attention and created controversy (Briske 1993) relative to reports of neutrality or simple compensation of productivity lost to grazing. Yet, the potential for grasses to compensate or overcompensate (Jaremo *et al.* 1999) to minimize the negative effects of tissue loss has obvious implications for energy flow, ecosystem function and the trophic dynamics of grasslands (Noy-Meir 1993).

Much of the controversy surrounding the potential for grazing optimization in grasslands stems from the empirical evidence provided. Criticisms of field studies purporting to show overcompensation in grasslands include claims that (i) data were collected at the incorrect scale, (ii) incorrect field methods were used, (iii) data were subject to calculation biases, and (iv) results and interpretations were rooted in faulty logic (Belsky 1986, 1987; Belsky *et al.* 1993; Biondini *et al.* 1991). Despite these criticisms, conditions that can lead to overcompensation have strong conceptual and theoretical support.

Theory predicts that there are two sets of conditions under which grazing may be expected to optimize ANPP in grasslands. de Mazancourt *et al.* (1998, 1999) argued that in productive grasslands where large losses of a limiting nutrient (such as N) may occur via frequent fire, grazing can reduce these losses by recycling of N through herbivores, and consequently increase productivity. Specifically, they predicted that grazing would be expected to increase ANPP in annually burned productive grasslands (de Mazancourt *et al.* 1999) as mediated indirectly by soil nitrogen availability. Alternatively, Milchunas and Lauenroth (1993) conducted a global analysis of grazing studies and suggested that in productive grasslands that are not burned, litter buildup can become excessive and reduce light needed for growth, and under these conditions grazing reduce the detritus layer and the associated light limitations to growth (Knapp and Seastedt 1986) and ANPP. Thus, these two perspectives provide opposing predictions for where overcompensation, as well as compensation, is more likely to occur in productive grasslands. Positive effects of grazing on ANPP should occur in annually burned grasslands if the 'nutrient conservation hypothesis' has identified the predominant mechanism. Alternatively, positive effects of grazing will be evident in unburned grassland if the 'light limitation hypothesis' is correct.

The goal of this study was to explicitly meet the conditions under which theory predicts that grazing should lead to optimization or overcompensation of ANPP (DeAngelis and Huston 1993) by assessing ANPP responses to grazing by large ungulates in both annually burned and unburned grasslands. ANPP–grazer interactions can be site specific and depend on herbivore type and grazing intensity (Milchunas and Lauenroth 1993). Thus, we quantified ANPP responses to grazing by large ungulates over 2 years in North American grassland and South African savanna where the long-term fire history (annual fire vs. fire exclusion) is known and currently under experimental control. Carefully controlled fire manipulation is necessary because past empirical studies of grazing effects on grassland ANPP have not accounted for fire history, perhaps contributing to inconsistencies in the evidence for grazing optimization of productivity. We also tried to alleviate many of the methodological concerns regarding data collection, calculation and interpretation biases that have plagued past studies (see Methods). This intercontinental comparative approach also allowed us to include ecosystems with two very different evolutionary histories of grass–grazer interactions, different types of grazers and years with differing amounts of rainfall (Buis *et al.* 2009).

METHODS

Study sites

The Konza Prairie Biological Station (KPBS) is a 3487 ha temperate grassland located in northeastern Kansas, USA (39°05′N, 96°35′W). KPBS is dominated by native, perennial C_4 grasses such as *Andropogon gerardii* and *Sorghastrum nutans* that account for the majority of herbaceous primary productivity (Knapp *et al.* 1998). Woody plants (C_3 shrubs and small trees such as *Cornus drummondii*, *Rhus glabra* and *Gleditsia triacanthos*) are common in sites not burned frequently and may comprise as much as 25% of the total plant cover (Briggs *et al.* 2005; Heisler *et al.* 2003). Maximum mean monthly air temperature in July is 27°C and annual precipitation averages 835 mm/year, with >70% falling as rain during the April–September growing season. Soils are fine textured, silty clay loams (Ransom *et al.* 1998). In 1988, bison (*Bos bison*) were reintroduced to portions of KPBS (see below).

Kruger National Park (KNP) encompasses nearly 2 million ha of protected savanna grassland in northeastern South Africa (22°25′–25°32′S, 30°50′–32°2′E). The south-central region of KNP (near Satara) where we conducted our research is co-dominated by a variety of C_4 grasses such as *Bothriochloa radicans*, *Panicum coloratum*, *Urochloa mosambicensis*, *Digitaria eriantha* and *Themeda triandra*, and C_3 woody species including *Acacia nigrescens*, *Sclerocarya birrea* and *Dichrostachys cinerea*. Maximum mean monthly air temperature occurs in January (29ºC) with mean annual rainfall of 518 mm (Venter *et al.* 2003) falling primarily during the months of

September–March. Although this site has precipitation levels below those at KPBS, a greater proportion of total annual precipitation falls during the growing season resulting in herbaceous ANPP and a general vegetation structure similar to KPBS. The dormant season (April–September) is mild, dry and frost free. The soils at the sites for our study are fine-textured clay and loam of basalt parent material (Venter *et al.* 2003). KNP supports many of the large herbivores such as elephant (*Loxodonta africana*), rhinoceros (*Ceratotherium simum*), African buffalo (*Syncerus caffer*), Burchell's zebra (*Equus burchelli*), blue wildebeest (*Connochaetes taurinus*), warthogs (*Phacochoerus aethiopicus*) and impala (*Aepyceros melampus*) that evolved in the grasslands of southern Africa (du Toit *et al.* 2003).

From a comparative perspective, both ecosystems share a common growing season climate, similar levels of herbaceous ANPP and are dominated by C_4 warm season grasses; however, North American grasslands are relatively young and experienced the loss of most of their original megaherbivore fauna in the Pleistocene, whereas the savannas of South Africa are a much older grassland-grazer system with most megaherbivores still present (du Toit *et al.* 2003; Gill *et al.* 2009).

Estimating ANPP under grazed and ungrazed conditions

In both North America and South Africa, we selected sites that had been consistently burned annually in the late dormant season or kept free of fire for ~20–50 years (KPBS and KNP, respectively) as well as being actively grazed by native megaherbivores for at least 20 years at KBPS and for much longer in KNP. This ensured that plant community composition, detrital accumulation and the nutrient status of the sites were representative of fire–grazing interactions expected for each site. At KPBS, bison were reintroduced in 1988 to a 1000 ha portion of the preserve that includes replicate watersheds burned at 1-, 2-, 4- and 20-year intervals. Current herd size is ~260 individuals and densities are based on a target of average consumption of 25% of ANPP with the overall grazing intensity being considered moderate (Knapp *et al.* 1999; Milchunas and Lauenroth 1993). In 1954, KNP established the Experimental Burn Plots (EBPs) to examine the effects of fire frequency (including fire exclusion, 1- and 3-year burn intervals) on plant and animal communities (Biggs *et al.* 2003). Each burn plot measures ~180 by 370 m (~7 ha). These plots are freely accessible to all herbivores. Impala, Burchell's zebra and blue wildebeest were the most abundant grazers observed during this study (DE Burkepile *et al.*, unpublished data), but warthog, rhinoceros and African buffalo are also important grazers on the EBPs. Also in the Satara region of KNP, a 900 ha permanent enclosure houses 80–90 adult African buffalo (*Syncerus caffer*). This enclosure (designated Buffalo Enclosure (KNP)) was erected in 2000 and was divided into six areas (100–200 ha each) including plots burned annually and plots left unburned. The African buffalo is a grazer considered functionally similar to bison (the primary grazer at KPBS) in terms of diet and body size (du Toit *et al.* 2003). We used the

unburned and annually burned areas in the buffalo enclosure to provide a direct comparison for determining the effects of a single large grazer species in KNP and KPBS, and to assess the effects of large herbivore diversity on ANPP at adjacent sites in KNP. For all three locations (Konza, the KNP EBPs and the KNP buffalo enclosure), grazing intensity can be quite variable within and between seasons and between years. To account for this variability, our experimental design included a total of 84 permanent and 168 moveable exclosures (MEs) deployed and moved periodically across these sites (see below).

To assess ANPP with large grazers removed (hereafter referred to as ungrazed areas), we established herbivore exclusion treatments in KPBS and KNP in 2006 (Buis *et al.* 2009) and measured ANPP in 2007 and 2008, when plant communities inside the exclosures were still similar to those outside (unpublished data). Exclosures were 7 m in diameter, 2 m tall and constructed of diamond mesh (5 cm mesh size) metal fencing material. Seven exclosures were established in two blocks of the two fire treatments—annually burned and unburned (*n* = 14 exclosures/treatment/site) at Konza, and in KNP in the EBPs and within the Buffalo enclosure. Because our focus was on ANPP responses of the herbaceous layer, exclosures were not located beneath trees or where dense shrub patches were present.

To examine ANPP in actively grazed grassland, we adapted methods from McNaughton *et al.* (1996) and Sala and Austin (2000). We used small (1 m²) temporary MEs and paired plots to estimate ANPP over approximately monthly time intervals during the growing season. Both the deployment of these exclosures and subsequent data analysis were specifically designed to offset criticisms of past methods (i.e. Biondini *et al.* 1991). Key features of this deployment and analysis were the following: (i) all ME and paired grazed plots were located randomly around the season-long grazing exclosures, (ii) we moved the MEs and established new paired plots 4–5 times (~1 month intervals) during the growing season to minimize errors of overestimation associated with high frequency sampling, and (iii) we included both positive and negative differences between MEs and paired grazed plots when calculating ANPP (Biondini *et al.* 1991; Sala *et al.* 1988).

We estimated ANPP in the presence of grazers by harvesting all aboveground plant biomass from one 0.1 m² (20 × 50 cm) quadrat within each ME and from the paired grazed plots (*n*= 2 ME and paired plots near each permanent exclosure) prior to moving them randomly within a 10 m radius of the permanent exclosure. We estimated ANPP in the absence of grazers by harvesting biomass in three 0.1 m² quadrats randomly located in each season-long large herbivore exclosure at the end of the growing season (Briggs and Knapp 1995). Thus, over the 2-year period, we harvested a total of 3192 quadrats to estimate ANPP. All herbaceous vegetation was harvested at ground level and separated it into grass, forb and previous year's dead biomass (present only in unburned areas). Samples were dried at 60°C to a constant weight. Due to the strong C_4 dominance, end of season (peak) biomass

Table 1: results from a mixed linear model ANOVA for the effects of year, fire (annually burned or no fire) or grazing (grazed or ungrazed) on total ANPP as well as ANPP for grasses and forbs at the three study sites

Site	Effect	df	Total		Grass		Forbs	
			F	P	F	P	F	P
Konza (KPBS)	Fire	2	1.88	0.1657	0.96	0.3922	0.63	0.5921
	Year	1	24.08	<0.0001	28.40	<0.0001	4.88	0.0291
	Fire × year	2	0.07	0.9362	0.01	0.9889	0.17	0.8463
	Grazing	1	4.86	0.0294	32.11	<0.0001	15.15	0.0002
	Fire × grazing	2	0.34	0.7140	0.57	0.5682	0.05	0.9527
	Year × grazing	1	5.21	0.0243	0.31	0.5815	10.52	0.0015
	Fire × year × grazing	2	0.25	0.7755	0.64	0.5310	1.85	0.1614
Kruger (KNP)	Fire	2	0.03	0.9699	0.30	0.7428	3.71	0.1520
	Year	1	0.94	0.3327	0.11	0.7422	6.95	0.0093
	Fire × year	2	0.67	0.5150	0.18	0.8351	6.11	0.0028
	Grazing	1	3.60	0.0597	4.35	0.0386	1.12	0.2917
	Fire × grazing	2	0.19	0.8299	0.17	0.8429	3.78	0.0250
	Year × grazing	1	0.38	0.5362	0.05	0.8233	2.64	0.1066
	Fire × year × grazing	2	2.45	0.0900	2.52	0.0834	4.82	0.0094
Buffalo Enclosure (KNP)	Fire	1	0.17	0.7201	0.24	0.6727	0.49	0.4891
	Year	1	4.47	0.0377	3.24	0.0758	3.68	0.0605
	Fire × year	1	0.48	0.4915	0.72	0.3978	1.24	0.2699
	Grazing	1	0.85	0.3595	1.16	0.2853	0.67	0.4169
	Fire × grazing	1	0.03	0.8696	0.01	0.9061	0.05	0.8275
	Year × grazing	1	2.29	0.1342	1.36	0.2463	4.19	0.0456
	Fire × year × grazing	1	0.00	0.9799	0.04	0.8366	1.22	0.2737

provides a reliable estimate of ANPP in the absence of grazing in both of these ecosystems (Knapp *et al.* 2006). For annually burned sites, total biomass harvested represents ANPP but for unburned sites, ANPP was calculated excluding the previous year's dead biomass. To calculate ANPP in actively grazed sites, we subtracted the biomass value from the paired grazed plots outside the ME at the beginning of each time interval from the value inside the exclosure at the end of the interval and summed all differences (positive and negative). We then added to this sum the residual biomass remaining at the end of the growing season. For estimating ANPP in the first interval of the growing season, we assumed biomass was zero since the MEs were established before significant ANPP occurred at the beginning of the growing season.

Statistical analysis

Statistical analyses of grazed and ungrazed ANPP were conducted using a mixed linear model (proc mixed, SAS 9.2, Cary, NC, USA). Fire treatment, year and grazing treatment were main effects with block and exclosure included as random effects. We did not use a repeated measures approach across years because exclosure size was sufficiently large to permit sampling in different locations. Exclosures were experimental units with replicate measurements (three replicates within each ungrazed exclosure and two replicates of MEs per ungrazed exclosure) averaged prior to analysis (n = 14/burn

treatment/grazing treatment/site). Because there were no significant effects of fire treatment in any site or year, we focus on year and grazing as main effects below. When significance in main effects or interactions were detected (P < 0.05) pairwise comparisons were made using the SAS 'lsmeans' procedure.

RESULTS

The 2 years of this study were similar with regard to growing season mean temperature (21.4 and 20.2ºC at Konza; 21.3 and 22.5ºC at Satara in 2007 and 2008, respectively), but growing season precipitation varied more so between years (659 and 860 mm at Konza; 540 and 434 mm at Satara, respectively). To test predictions from the nutrient conservation versus light limitation hypotheses we initially compared the impact of grazing on ANPP in sites burned annually versus those with no fire (Table 1). When analyzed by fire frequency (annually burned vs. unburned) we detected no significant effects (P > 0.05) of grazing on ANPP (positive or negative) in either year or at any of the three sites (Fig. 1). This was also the case for grass and forb ANPP (Table 1). This compensatory response occurred during both moderately wet and relatively dry growing seasons, and with grazing intensities ranging from 10 to 60% across all sites and over 2 years (estimated as the difference between end of season biomass inside the permanent exclosures and the grazed plots outside). Regression
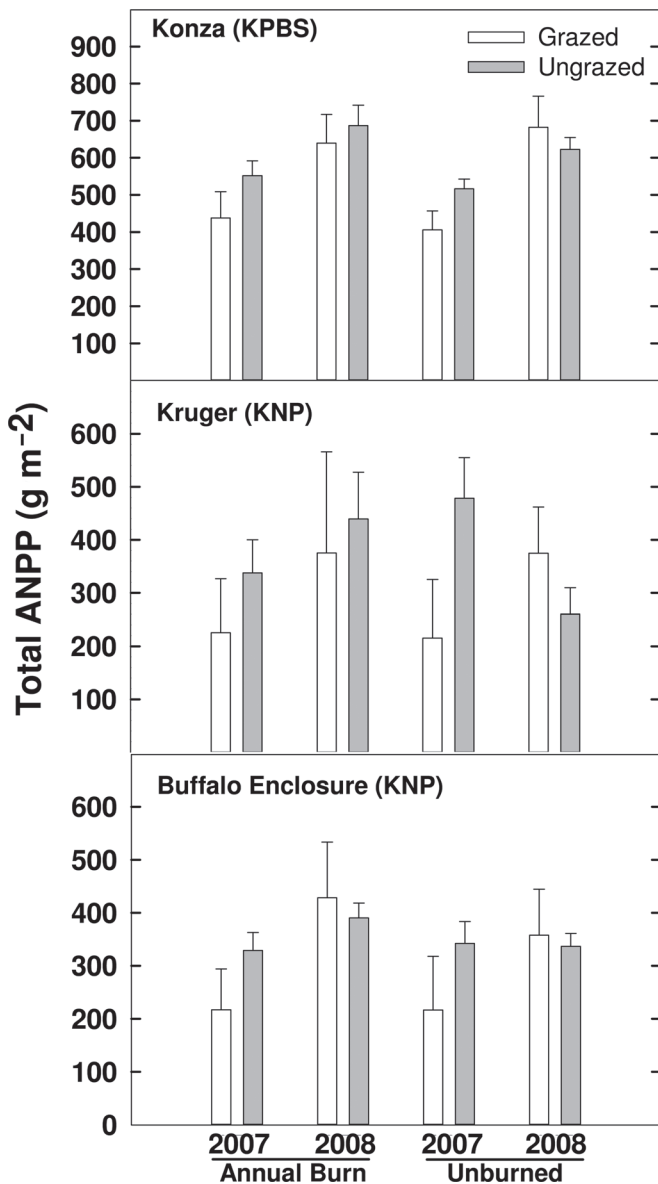
Figure 1: effect of grazing on total ANPP over 2 years in annually burned and unburned sites. Estimates of ungrazed ANPP are from peak (end of season) biomass harvest from permanent exclosures erected in 2006 and grazed ANPP estimates are based on summing approximately monthly intervals of biomass production in MEs (see Methods). Top: results from Konza Prairie (KPBS,; USA) watersheds grazed by North American bison. Middle: results from KNP (South Africa) experimental burn plots (Satara) grazed by a diverse suite of herbivores. Bottom: results from a Buffalo enclosure in KNP (Satara) grazed by African buffalo. Error bars represent 1 standard error. There were no significant differences between fire treatment or grazing in any year or site.

analyses revealed no relationship between estimates of grazing intensity and the effect of grazing on ANPP across these sites. In general, estimates of ANPP in both grazed and ungrazed conditions were more variable in KNP than at KPBS (Fig. 1) consistent with previous estimates of ANPP at these same sites (Buis *et al.* 2009).

With fire treatments combined, we did detect significant reductions (undercompensation) in ANPP due to grazing for total and grass ANPP at KPBS (Fig. 2). Analyses for total ANPP revealed significant main effects of year ($P < 0.0001$) and grazing ($P = 0.0294$) in addition to a year-by-grazing interaction ($P = 0.0243$), whereas grass ANPP differed by year ($P < 0.0001$) and grazing ($P < 0.0001$; Table 1). The negative effects of grazing on ANPP occurred for both years for grass ANPP (2007: $P < 0.0001$; 2008: $P = 0.0002$), but just in the drier year (2007) for total ANPP ($P = 0.0019$). In contrast, there was a positive response of forbs to grazing at KPBS with significant effects of year ($P < 0.0291$), grazing ($P = 0.0002$) and a year-by-grazing interaction ($P = 0.0015$; Table 1). Year 2008 was the only year with a significant increase in forb ANPP in response to grazing ($P < 0.0001$). There was complete compensation of total ANPP in 2008 due to high forb ANPP in grazed areas during this relatively wet growing season.

In KNP, we detected a significant decrease in grass ANPP ($P = 0.0386$), and a marginally significant decrease in total ANPP ($P = 0.0597$) in response to grazing (Fig. 3; Table 1). Forb ANPP was highly variable with no significant effect of grazing detected despite strong trends for increased forb ANPP in 2008 and when years were combined (Fig. 3). Overall, with the exception of grass ANPP, compensation (no significant difference between grazed and ungrazed ANPP) was most often observed. Finally, in the buffalo enclosures in KNP (Fig. 4) complete compensation was found for both total and grass ANPP as no significant main effects or interactions were detected (Table 1). Forb production was highly variable with no main effects detected, but there was a significant grazing-by-year interaction ($P = 0.0456$) and there was a strong trend for grazing to increase forb ANPP in 2008.

DISCUSSION

Mesic temperate grasslands and sub-tropical savannas share strongly seasonal climates, frequent fire and grazing by large herbivores as important drivers of ecosystem structure and function (Knapp *et al.* 2006). In particular, large herbivores exert significant influence on the function of these ecosystems and can directly and indirectly impact net primary productivity, one of the most fundamental of ecosystem processes (McNaughton *et al.* 1989). However, these effects can be variable in both space and time, and Briske (1993) noted that both compensatory growth and overcompensation in response to herbivores have been documented. Yet, compensatory growth *does not* occur in all species or in response to all combinations of biotic or environmental variables. Briske (1993) suggested that the appropriate question to ask with regard to the impact of herbivores on ANPP is 'With what frequency and magnitude does compensatory growth occur in a diversity of grazed systems?' We adopted this perspective and opted to test specific predictions from theory regarding the environmental conditions under which we would most likely be able to detect compensatory growth, or even
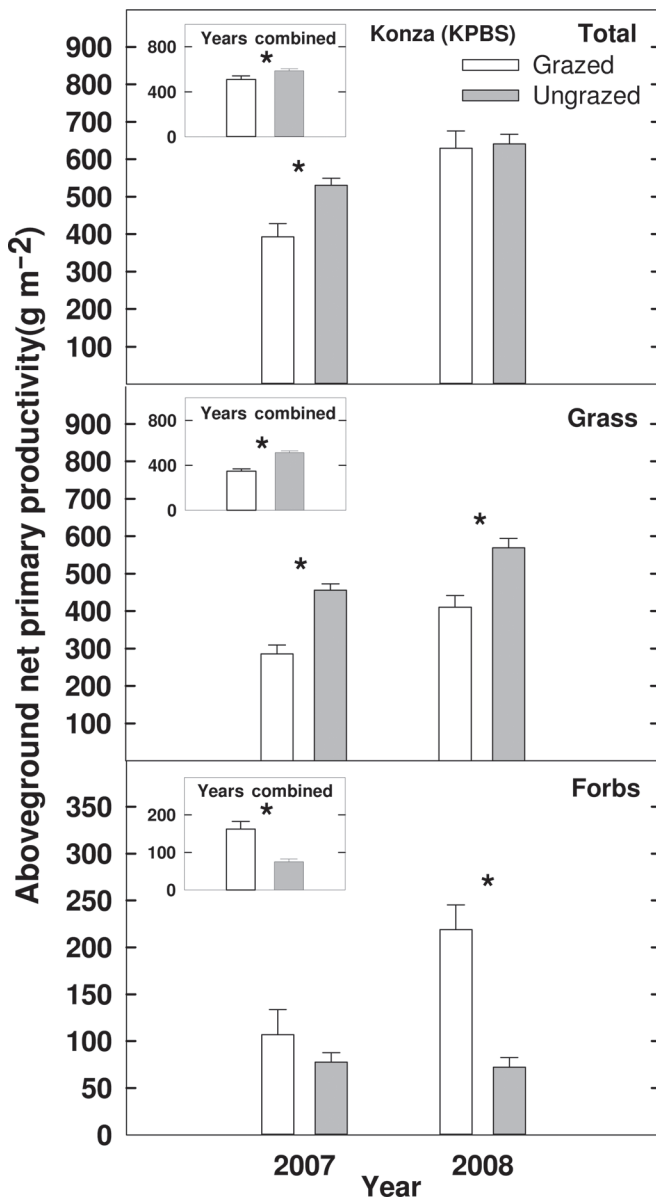
Figure 2: effect of grazing on total ANPP for 2 years at Konza Prairie (KPBS). Data were combined for burned and unburned sites and are presented for each year separately or combined for both years (inset) for total, grass and forb components. Error bars represent 1 standard error and significant differences (*P* < 0.05) between grazing treatments are indicated by asterisk (*). Although not indicated, 'year' was significant for total, grass and forb ANPP.

overcompensation, in a productive North American grassland and South African savanna. By doing so, we can better identify the mechanisms responsible for the diversity of responses to grazing that have been reported in the past (Bagchi and Ritchie 2011; Noy-Meir 1993). Specifically, by focusing on annually burned and unburned grasslands in sites with levels of resources that should allow for compensation or even overcompensation (Frank and McNaughton 1993; Machinski and Whitham 1989) we tested two opposing predictions: (i)

that positive effects of grazing on ANPP would most likely occur in annually burned grasslands (nutrient conservation hypothesis; de Mazancourt *et al.* 1998, 1999) or (ii) that positive effects of grazing on ANPP would most likely occur in unburned grassland (light limitation hypothesis; Knapp and Seastedt 1986; Milchunas and Lauenroth 1993).

The 2-year duration of this study also allowed us to compare ANPP responses to grazing in years that differed moderately in growing season precipitation. Growing season rainfall increased by 30% from year 1 to 2 at KPBS, whereas it decreased by 20% from year 1 to 2 at KNP. At KPBS, ANPP responded positively to greater rainfall but in KNP variability in ANPP was much greater within years and not consistent with rainfall variation across years, suggesting that other factors such as timing of rainfall events are particularly important in these grasslands (Swemmer *et al.* 2007). When we compared ANPP in actively grazed areas to ANPP within adjacent grazing exclosures, we detected no significant differences regardless of fire history. Thus, whether annually burned or left unburned, these three grassland sites compensated completely for biomass lost to herbivores. This was despite 2 years of study in 2 very different grass-dominated ecosystems, across years with significantly different rainfall patterns, and with three different suites of native large ungulate grazers (bison at KPBS, and in KNP either diverse herbivores in the EBPs or a single-species herd of African buffalo).

Although these data do not support specific predictions from either the nutrient compensation or light limitation hypotheses, the trend towards either compensation or undercompensation in annually burned sites is consistent with the results of Turner *et al.* (1993) who reported complete compensation of biomass removed in KPBS grasslands grazed by cattle, with undercompensation occurring in a drought year. This observation and the trend in 2008 for overcompensation in grazed unburned sites provide limited support for the light limitation hypothesis. Significantly greater light availability at ground level was measured in these grazed versus ungrazed treatments previously (Buis *et al.* 2009), thus grazing increased this resource. We did not assess N availability inside the exclosures versus outside in this study, but previous studies at KPBS have shown that N availability can be significantly decreased by fire with no grazing in as little as 2 years (Blair 1997). The lack of difference in ANPP between burned and unburned sites suggests that soil N did not mediate grazing responses across these two extremes in fire frequency.
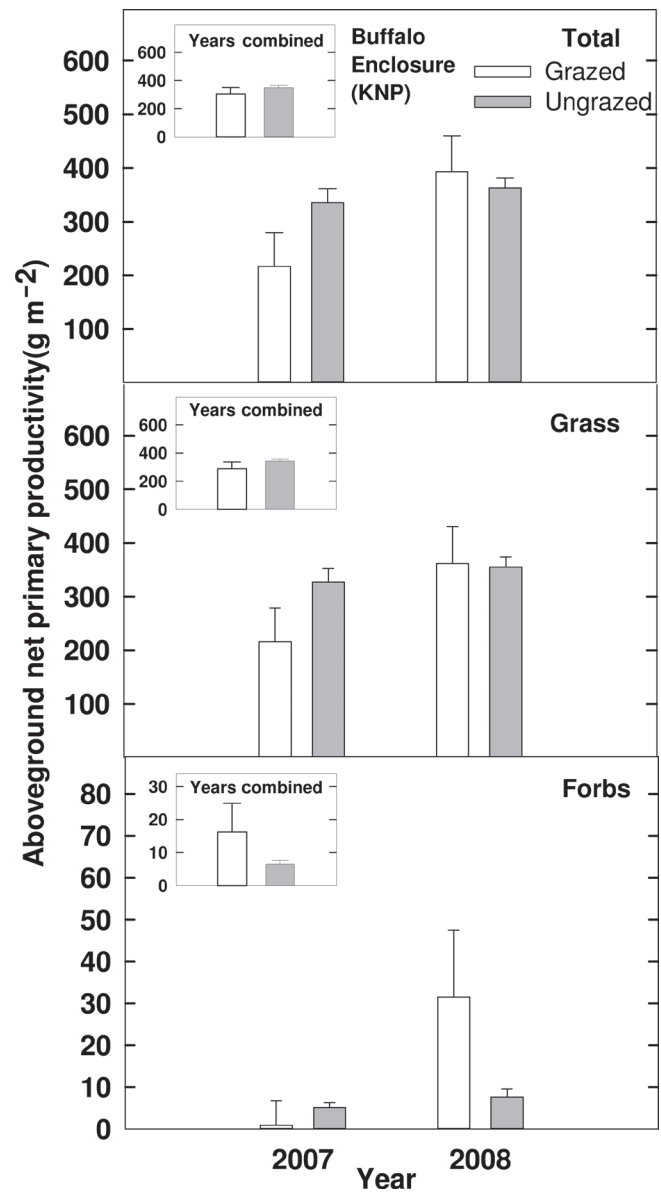
When burned and unburned sites were combined to assess the main effects of grazing, patterns were broadly similar at all three sites. In general, either complete compensation or undercompensation of total and grass ANPP was evident, whereas forb ANPP showed evidence of overcompensation at all three sites, at least in the second year of study. Significant differences in ANPP between grazed and ungrazed sites were most commonly detected at KPBS and the variability associated with estimates of ANPP was lowest at this site (see error bars, Fig. 1). Reduced variability in ANPP estimates at
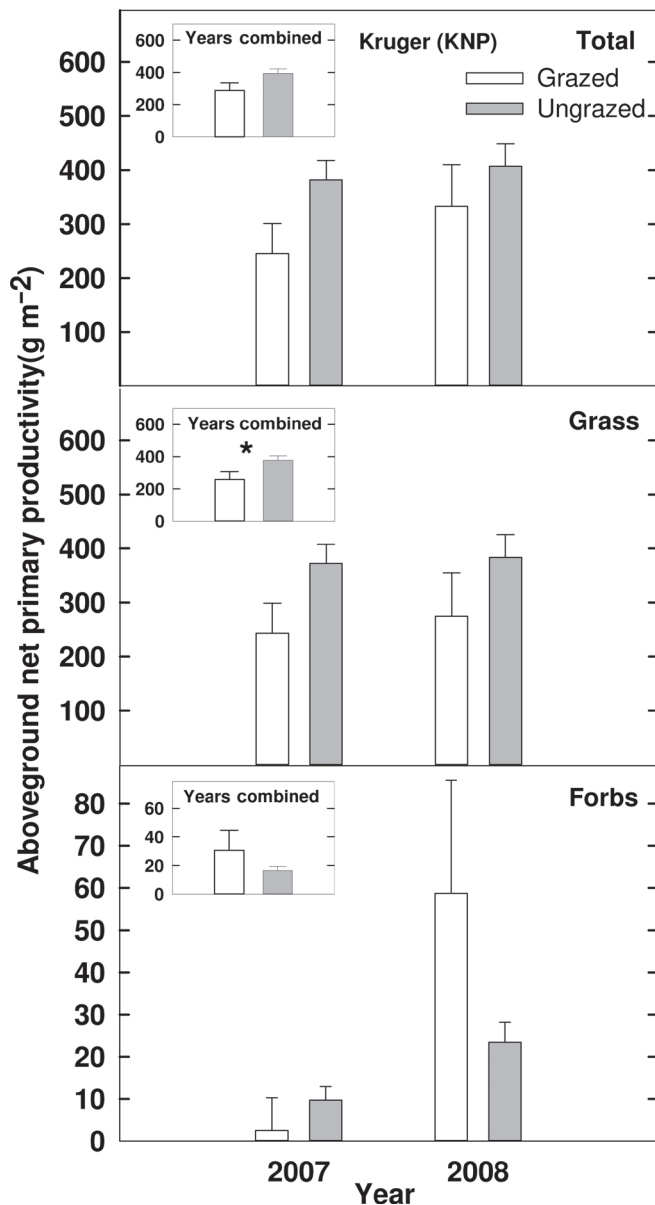
Figure 3: effect of grazing on total ANPP for 2 years in KNP. Data were combined for burned and unburned sites and are presented for each year separately or combined for both years (inset) for total, grass and forb components. Error bars represent 1 standard error and significant differences ($P < 0.05$) between grazing treatments are indicated by asterisk (*). Although not indicated, the effect of grazing was marginally significant for total ANPP when years were combined ($P = 0.0597$).

Figure 4: effect of grazing on total ANPP for 2 years in the Buffalo Enclosure in KNP. Data were combined for burned and unburned sites and are presented for each year separately or combined for both years (inset) for total, grass and forb components. Error bars represent 1 standard error.

KPBS is likely due to the more uniform distribution of grass tillers in this strongly rhizomatous sod-forming grassland. Furthermore, reductions in grass ANPP and increases in forb ANPP with grazing are consistent with responses in plant community structure from KPBS (Collins *et al.* 1998; Veen *et al.* 2008) and regional-scale patterns (Bakker *et al.* 2006).

One explanation for why we detected only compensation or undercompensation in KPBS and KNP whereas overcompensation has been measured in the Serengeti and Yellowstone National Park (Frank *et al.* 1998) is that these latter sites are characterized by migratory herds and periods of intense grazing. The grazing patterns of resident herds in KBPS and KNP likely differ substantially from migratory herds. Several studies have shown that either undercompensation or compensation is more likely to occur in grasslands that have been repeatedly grazed versus those that have been rested from grazing the prior year (Briske 1993; Kirkman 2002; Turner *et al.* 1993). Both the grasslands at KPBS and the savanna grasslands in KNP have a history of grazing by resident large ungulate herds.

The pattern of increased forb ANPP with grazing (particularly evident when combined across years, see insets of Figs 2–4) suggests a general pattern of competitive release from dominance by the grasses at all three sites when grazing occurs. This increase in forb ANPP under grazing at all three sites is consistent with the finding of a field experiment that clipping of grasses strongly reduced their below-ground competitive effects on neighbours resulting in competitive release of a phytometer species (Tedder *et al*. 2011). Finally, forb ANPP at KPBS was as much as 6-fold greater in grazed sites at KPBS than in either site in KNP. This is consistent with previous studies from ungrazed sites (Buis *et al*. 2009) and suggests that relatively substantial differences in plant community structure did not alter ecosystem scale functional responses (ANPP) to grazing.

In summary, despite strong theoretical and conceptual arguments for nutrient conservation and light limitation as mechanisms that may promote overcompensation of biomass lost to grazers, our data provided little support for either hypothesis. We were unable to detect overcompensation in either annually burned or unburned sites, or when sites and years were combined. Complete compensation in total ANPP was most often detected in these mesic grasslands and savannas with both mechanisms potentially important. Undercompensation occurred in growing seasons with reduced precipitation, consistent with the hypothesis that compensatory growth is more likely to occur when resources are available to facilitate re-growth (Machinski and Whitham 1989). Grasses responded most similarly in these two different grass-dominated ecosystems, with undercompensation of this key functional group occurring overall at both sites. Forb ANPP was quite variable, likely due to the heterogeneous spatial distribution of this functional group, but when responses were detected, forb ANPP was increased by grazing, likely due to competitive release, and these responses in general helped to offset the grass responses with regard to total ANPP. Overall, the similarity of responses of ANPP to grazing suggests that despite differences between sites and years, and with three different types of grazing herds, compensation of total biomass lost to herbivores is the most common response characterizing grazing–ANPP relationships in these productive grass-dominated ecosystems.

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