

# Interactive Effects of Ungulate Herbivores, Soil Fertility, and Variable Rainfall on Ecosystem Processes in a Semi-arid Savanna

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## ABSTRACT

Large herbivores can both positively and negatively affect primary productivity and rates of nutrient cycling in different ecosystems. Positive effects of grazers in grasslands have been attributed to migratory behavior of the dominant ungulate species and soil fertility. We studied the effects of grazers on aboveground net primary productivity (ANPP) and N cycling on central Kenyan rangeland characterized by intense, chronic grazing by a mixed community of cattle and resident native ungulates. Exclosure studies conducted at high and low levels of soil fertility showed that both soil fertility and annual rainfall patterns mediate the effects of grazers on ANPP and N cycling. In a low-rainfall year with short (1 month) growing seasons, grazers reduced aboveground productivity regardless of soil nutrient availability. However, in a high-rainfall year with a 5-month growing season, grazers increased ANPP on nutrient-rich glades and suppressed ANPP on nutrient-poor bushland sites. Concomitant studies of grazer effects on N cycling revealed complex interactions with the seasonal pattern of N-mineralization and inorganic N availability. Grazers increased the size of the inorganic N pool available to plants at the onset of the growing

season, particularly in nutrient-rich glades. However, grazers also decreased N mineralization rates at all sites early in the growing season. Measures of N availability via ion-exchange resin bags suggested that the combined effects of grazers on inorganic N pool fluctuations and N-mineralization rates resulted in a net increase in N availability at glade sites and a net decrease in N availability at bushland sites. The net effect of grazers on soil N availability mirrored grazer effects on ANPP in the high-rainfall year. Overall, our results suggest that grazer effects on N dynamics are closely linked to effects on productivity and resilience to drought. Furthermore, even under optimal conditions of high soil fertility and above-average rainfall, grazer promotion of ANPP in this chronically grazed system dominated by resident ungulates was small compared to systems dominated by migratory ungulates.

**Key words:** cattle; grazing ecosystems; grassland; impala; inorganic nitrogen; nutrient cycling; non-equilibrium rangelands; phosphorous; wildlife management.

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## INTRODUCTION

Research on terrestrial ecosystems has recognized the regulatory effect large mammalian herbivores can exert over the flow of energy and nutrients (Pastor and others 1993; McNaughton and others

1997; Frank and Groffman 1998; Ritchie and others 1998; Knapp and others 1999). However, the direction of this effect can differ dramatically among ecosystems, and a wide range of underlying factors may determine how herbivores influence ecosystem processes (Hobbs 1996; Augustine and McNaughton 1998; Bardgett and Wardle 2003). For example, moose (*Alces alces*) in boreal forests influence ecosystem processes due to their role as a selective plant-removal agent, even when the overall level of primary productivity consumed is small (Bryant and others 1991; Pastor and others 1993). Empirical studies combined with model analyses (Pastor and Cohen 1997) suggested that in most ecosystems, herbivory will reduce primary productivity and inhibit nutrient cycling rates as the system becomes dominated by slow-growing, unpalatable plants. This conclusion is supported by studies from some savannas where selective consumption of palatable grasses by cattle drives the system toward dominance of spinescent, woody species (reviewed by Archer 1995) or unpalatable grasses (Brown and Stuth 1993; Anderson and Briske 1995). Selective herbivory can also limit the abundance of nitrogen-fixing species, a key functional group in many ecosystems, thereby reducing soil nitrogen availability (Ritchie and others 1998).

In contrast, studies of several ecosystems supporting abundant populations of large, vertebrate herbivores show that herbivory can stimulate primary productivity, rates of nutrient cycling, and hence secondary productivity (Cargill and Jefferies 1984; McNaughton 1985; Bazely and Jefferies 1985; Shariff and others 1994; Frank and Groffman 1998; McNaughton and others 1997; Frank and others 2002). In these ecosystems, the capacity for plants to regrow rapidly between bouts of herbivory and the relative absence of chemical plant defenses allows a large proportion of primary production to be processed through herbivores and the associated microbial communities of their digestive systems. Herbivores also adjust their local density in response to plant productivity and nitrogen content such that temporally and spatially variable pulses of high plant productivity are transferred to herbivores (Frank and others 1998).

Such variation among ecosystems in the effects of vertebrate herbivores, and the wide range of factors that could influence plant-herbivore interactions, have limited the development of generalized inferences concerning the role of large herbivores in ecosystems (Bardgett and Wardle 2003). Migratory behavior of ungulate species in the Serengeti and Yellowstone National Parks in response to spatiotemporal gradients of plant pro-

ductivity and nutrient content has been implicated as a key mechanism maintaining the functional properties of grazing ecosystems (Frank and others 1998). This conclusion is supported by the long-term declines in primary productivity, nutrient retention, and secondary productivity that some savanna ecosystems have experienced in response to increased densities and reduced migratory behavior of domestic livestock (Sinclair and Fryxell 1985; le Houerou 1989).

Another proposed determinant of herbivore effects on ecosystems is soil fertility (Ritchie and others 1998; Bardgett and Wardle 2003). Both theoretical arguments (Coley and others 1985) and some empirical evidence (Bryant 1987; Bryant and others 1989; Scholes and Walker 1993) indicate that nutrient availability in an ecosystem determines the degree to which plants invest in chemical defenses on both evolutionary and ecological time scales to prevent herbivory. Laboratory experiments also demonstrate that critical levels of nutrient supply are required for grasses to tolerate simulated herbivory without a reduction in productivity (Chapin and McNaughton 1989; Wegener and Odasz 1997; Hamilton and others 1998). Bardgett and Wardle (2003) outlined three key mechanisms by which herbivores influence soil processes in ways that feed back to plant productivity: (1) alteration of the quantity of resource inputs to soil (exudation, litter inputs), (2) alteration of the quality of resource inputs to soil, and (3) long-term alteration of plant community composition. Based on the interaction between these mechanisms, they predicted that "positive effects of herbivory on soil biota and soil processes are most common in ecosystems of high soil fertility and high consumption rates" (Bardgett and Wardle 2003, p. 2258). They also identified comparative studies of herbivore impacts on above- and belowground processes across ecosystems of varying productivity as a key research priority.

Climate is also a key determinant of the role large herbivores play in ecosystems. Traits that enable plants to tolerate herbivory, such as basal meristems, also confer tolerance to drought, such that increasingly arid ecosystems can be increasingly tolerant of defoliation (Coughenour 1985; Milchunas and others 1988). Ellis and others (1993) suggested that arid and semi-arid systems where the annual coefficient of variation in rainfall exceeds 30% are best described by non-equilibrium relations between plants and herbivores. They argued that annual fluctuations in plant production become so great that herbivore populations are incapable of tracking productivity and hence have

no significant effects on plant dynamics (Ellis and others 1988, 1993). This hypothesis has been contested on theoretical (Illius and O'Connor 1999, 2000) and empirical grounds (Oba and others 2000, Fynn and O'Connor 2000), and the degree to which large herbivores influence aboveground net primary productivity (ANPP) in climatically variable ecosystems remains unclear.

We examined the interactive effects of ungulate grazing, soil fertility, and annual variability in rainfall on ecosystem processes at the Mpala Research Centre in central Kenya. This ecosystem is appropriate for studying such interactive effects for two reasons. First, annual rainfall is low and variable (mean = 508 mm, 1 SD = 226 mm over the past 30 years). Thus the coefficient of variation (44%) exceeds the level suggested by Ellis and others (1993) as indicative of non-equilibrium dynamics. Second, long-term cattle management practices in the region have created a mosaic of 0.5–1.0 ha patches of nutrient-enriched grassland dispersed throughout the nutrient-poor bushland landscape (Augustine 2003a). Nutrient-rich patches in the landscape are created by the large quantities of animal dung and urine that concentrate in overnight livestock corrals or "bomas". Livestock bomas are subsequently abandoned and colonized by a unique plant community as the manure layer becomes mixed with mineral soil (Young and others 1995; Augustine 2003a). Soil carbon and nutrient content declines during the first 4 decades after boma abandonment, but bomas greater than 40-years old (referred to as "glades" hereafter) remain enriched in total soil C, N and P, possibly for centuries (Augustine 2003a; Blackmore and others 1990). The difference in nutrient content between glade and surrounding bushland soils within an otherwise geologically and climatically homogenous landscape provides a unique opportunity to examine the degree to which soil fertility mediates the effects of herbivores on grassland productivity and nutrient cycling. Here, we report on results of enclosure experiments conducted with herbaceous communities growing on nutrient-rich (glade) and nutrient-poor (bushland) soils during drought, dry and wet years to examine the effects of grazers on inorganic soil nutrient availability and grassland productivity.

## STUDY AREA

All research was conducted at the Mpala Research Centre and Mpala ranch (Mpala) which encompasses 190 km<sup>2</sup> in central Kenya (37°53'E, 0°17'N). The landscape is underlain by well-

drained, moderate to very deep, friable sandy loams developed from metamorphic basement rocks (Ahn and Geiger 1987). Topography consists of gently rolling hills and occasional granitic inselbergs. During this study, mean annual rainfall (averaged across three rain gauges maintained at each of the large-scale enclosure study sites) was 410 mm in 1999, 296 mm in 2000 and 658 mm in 2001. Rainfall in 1998 (measured at a single gauge near the center of the study area) was 702 mm. Rainfall in 2000 was the second lowest recorded during 1972–2001. Rainfall occurs in a trimodal fashion with wet seasons typical during April–May, August, and October, and a consistent dry season during January–March. Studies of plant and nutrient dynamics were initiated in the January–March dry season and encompassed wet seasons during April–August in 1999, 2000 and 2001. For further details on monthly patterns of precipitation during 1999–2001, see Augustine and McNaughton (2004).

Young and others (1995) described vegetation at Mpala as a two-phase mosaic consisting of glades (short-grass patches lacking woody vegetation; 1% of the landscape) distributed within a background *Acacia*-dominated bushland community (99% of the landscape). Aerial photographs of Mpala taken in 1961 and 1969 were used to identify long-term glades present since 1961. Glades are dominated by a short-statured sward of *Cynodon plectostachyus* and include the annual forb *Tribulus terrestris*, the sedges *Cyperus blysmoides* and *Cyperus cristatus*, and the grass *Sporobolus pellucidus*. In the surrounding bushland community, the woody layer is dominated by *Acacia brevispica*, *A. mellifera*, and *A. etbaica* with average shrub canopy cover of 28%, and the herbaceous layer is dominated by the perennial grasses *Digitaria milaniana*, *Cynodon dactylon*, *Pennisetum mezianum*, and *Pennisetum stramineum* (Augustine 2003b). Plant nomenclature follows Polhill (1972–1982). Fire may previously have been an important component of Laikipia's savannas, but has been actively suppressed by ranch managers since European settlement. No large-scale fires are known to have affected the study area in recent decades.

Since at least 1800, the Laikipiak Maasai occupied and maintained livestock at Mpala, but most Maasai left the area following a treaty with the British in 1911 (Young and others 1995). Since that time, Mpala and surrounding areas have primarily been privately-owned rangeland. At Mpala, livestock have been managed for market production using traditional pastoral herding methods, with both Maasai and Turkana herders hired to maintain the cattle. The ranch is not fenced. Between 1990

and 2000, approximately 1,400–3,100 cattle have been maintained at Mpala, with peak numbers occurring after high rainfall in 1998 ( $15.7 \text{ km}^{-2}$ , equivalent to  $4,600 \text{ kg km}^{-2}$ ) and minimum numbers after the severe drought in 2000 ( $7.1 \text{ km}^{-2}$  equivalent to  $2000 \text{ kg km}^{-2}$ ).

The most common native grazers and mixed-feeders are impala (*Aepyceros melampus*), zebra (*Equus burchellii*), scrub hares, (*Lepus saxatilis*), waterbuck (*Kobus ellipsiprymnus*), buffalo (*Syncerus caffer*), and eland (*Taurotragus oryx*). Impala occurred at a mean density of  $20.3 \text{ km}^{-2}$  during this study, whereas all other ungulates occurred at densities less than  $1 \text{ km}^{-2}$ . Native predators include spotted hyaena (*Crocuta crocuta*), lion (*Panthera leo*), leopard (*Panthera pardus*), and wild dogs (*Lycan pictus*).

## METHODS

### Grazer Exclusion Experiments

Two enclosure experiments were used to examine the effects of grazers on ANPP and soil N dynamics in glade and bushland communities. Although the comparison of glade and bushland dynamics is not an experimental treatment, our approach follows the design of previous studies of ungulate herbivory in grassland ecosystems, where grazer effects are measured in different plant communities and under varying abiotic conditions (for example, McNaughton and others 1997; Frank and Groffman 1998; Bardgett and Wardle 2003). In this study, we specifically compare ecosystem processes at paired glade vs. bushland sites that occurred at the same topographic position, had the same soil texture, and received the same rainfall inputs. The first experiment employed small enclosures (see details below) that were constructed during November–December 1998 at four glade and four bushland sites, and monitored during the March–August growing seasons in 1999 and 2000 (1 and 2 years after enclosure construction). The second experiment employed large enclosures (see details below) that were constructed during June–July 1999 at 3 glade and 3 bushland sites, and monitored during the March–August growing season in 2001 (2 years after enclosure construction).

**Small Enclosure Experiment.** This experiment was conducted at four paired glade and bushland study sites, where effects of grazers on productivity were evaluated by measuring herbaceous productivity in grazed areas by the moveable grazing cage method (McNaughton and others 1996) and comparing measures to productivity inside permanent enclosures. At each glade, we established a  $50 \times 50 \text{ m}$

study area where we monitored one randomly-located  $4 \times 2 \text{ m}$ , permanent wire-mesh enclosure, four  $1 \text{ m}^2$  control (grazed) plots, and four plots protected with  $1 \text{ m}^3$  moveable grazing cages (McNaughton and others 1996). Bushland sites were all located approximately 200 m from the paired glade site and occurred at the same topographic position as the nearby glade. At each bushland site, we established a  $50 \times 50 \text{ m}$  study area where we conducted measurements at seven randomly-selected locations between shrub canopies (one permanent  $2 \times 2 \text{ m}$  wire-mesh enclosure, three  $1 \text{ m}^2$  grazed control plots, and three plots protected with  $1 \text{ m}^3$  moveable grazing cages) and seven randomly-selected locations beneath shrub canopies (one permanent  $2 \times 2 \text{ m}$  wire-mesh enclosure, three  $1 \text{ m}^2$  grazed control plots, and three plots protected with  $1 \text{ m}^3$  moveable grazing cages). Only shrubs with canopy architecture that permitted grazing beneath them were used in this study. At all bushland study sites, the herbaceous community between shrubs was dominated by *Cynodon dactylon*; beneath-shrub plots were dominated by *Cynodon dactylon* at two sites, by *Cynodon* and *Digitaria milanijiana* at one site, and by *D. milanijiana* and *Pennisetum mezianum* and at the fourth site. Data from beneath- and between-shrub plots were pooled, giving six moveable cages and six controls monitored per bushland site per month. Biomass in moveable cages, control plots, and permanent enclosures was measured every 24–28 days early in the growing season, 28–30 days late in the growing season, and 30–45 days during dry seasons, with measurements conducted during March–August in 1999 and 2000. Biomass was measured by canopy interception with 49 pins  $0.5\text{-m}^{-2}$  passed through the canopy at a  $45^\circ$  angle. The canopy interception method was calibrated with clipped plots for each of five groups: stoloniferous grasses, bunchgrasses, *Pennisetum mezianum*, thin-leaved grasses, and forbs (see Augustine 2003b for regression equations).

In the small enclosure experiment, effects of large herbivores on soil inorganic N pool size were measured in May, 2000. At each glade, four soil cores (5 cm dia, 0–15 cm depth) were collected from inside and outside the permanent enclosure. At each bushland site, we collected 4 cores inside enclosures and 8 cores outside enclosures, with sampling stratified between and beneath shrub canopies. Soil cores were placed on ice in a cooler and returned to the Mpala laboratory where a 15 g subsample was extracted with 1 M KCl within 48 h. Another 15 g subsample was used to measure gravimetric moisture content. KCl extracts were

frozen until shipment to Syracuse University, where they were analyzed for  $\text{NO}_3^-$  and  $\text{NH}_4^+$  concentrations by continuous flow analysis (Lachat Quikchem AE, Milwaukee, WI). Soil cores were also collected at the beginning of the experiment in November 1998 (4 per glade and 8 per bushland site) and analyzed for total C and N by Dumas combustion with a Carlo-Erba CN Analyzer, (Milan, Italy), total soil P by inductively-coupled plasma spectroscopy (Leman Labs PS3000, Hudson, MA, USA), and soil texture by the hydrometer method.

**Large Exclosure Experiment.** The large-scale exclosure experiment was initiated in 1999 because the small-scale exclosure experiment did not allow sufficient space for monthly, destructive soil sampling methods (N-mineralization and N adsorption to resin bags). In 1999, two, paired 0.5 ha ( $70 \text{ m} \times 70 \text{ m}$ ) plots were established at each of 3 glade and 3 bushland study sites. For each pair of plots, one was randomly selected and protected with an 11-strand, 3-m tall electrified fence that excluded all large herbivores ranging in size from hares to elephants. Fences followed the design of "Young and others (1998)", with additional mesh and electrified wires from 0 to 0.5 m in height that effectively excluded dik-dik and hares. Herbaceous ANPP was measured at each site during March–August 2001. Glades were monitored using six  $1\text{-m}^2$  plots in the permanent exclosure, six grazed control plots, and six moveable grazing cages per site. Bushland study sites in this large-exclosure experiment were dominated by perennial stoloniferous grasses between shrub canopies (*Cynodon dactylon* at sites 1 and 2; *Digitaria milanjiana* at site 3) and bunchgrasses beneath shrub canopies (*Enteropogon macrostachyus* at sites 1 and 2; *Cymbopogon pospischilii* and *Themeda triandra* at site 3). At bushland sites, there were six plots per treatment (grazed, temporary cages, permanent exclosure) beneath shrubs and six plots per treatment between shrub canopies.

During 2001, three measures of soil inorganic N availability were conducted inside and outside the large ( $70 \times 70 \text{ m}$ ) exclosures: (1) inorganic N pool size, (2) N-mineralization rates, and (3) inorganic N adsorption to ion-exchange resin bags (Binkley and Hart 1989). On each of the six sampling dates when herbaceous biomass was measured during March–August, 2001, we collected 5 cm dia  $\times$  15 cm deep bulk soil cores for determination of inorganic nutrient pools (6 cores per glade per grazing treatment, 12 cores per bushland site per grazing treatment with bushland sampling stratified between and beneath shrubs). We also incubated the

same number of cores *in situ* in 5 cm dia  $\times$  15 cm deep PVC tubes until the subsequent measurement interval (McNaughton and others 1997). Subsamples (15 g) of initial and incubated soil cores were extracted with 1 M KCl within 48 h of collection. N-mineralization rates were calculated as the difference in  $(\text{NH}_4^+ + \text{NO}_3^- - \text{N})$  between initial and incubated soil cores. Due to occasional extreme soil N values associated with urine inputs, in all analyses of N mineralization rates, samples exceeding the mean by  $\pm 3$  standard deviations were excluded from analyses. Additional studies that quantified N lost from mineralization tubes via leaching showed that leaching was a function of initial soil inorganic N pool size (at the beginning of the incubation) and rainfall (Leached N ( $\text{g m}^{-2}$ ) =  $0.00536 \times (\text{mm rain}) + 0.1315 \times (\text{initial g mineral N m}^{-2}) - 0.1977$ ;  $r^2 = 0.53$ ,  $t_{\text{rain}} = -3.74$ ,  $P = 0.0003$ ;  $t_{\text{mineralN}} = 8.99$ ,  $P < 0.0001$ ; see Augustine and McNaughton 2004) and mineralization values during months with greater than 40 mm rain were corrected for leaching using this equation. Net N-mineralization over the entire growing season was the sum of all months with positive mineralization rates. We also conducted monthly dung-group counts on eight 20-m transects (cleared after each count) at each study site for each herbivore species during 2001, and used these counts combined with measures of mean dung-group size and N content to estimate the monthly rate of N deposition as dung. Urine-N deposition was calculated from dung deposition based on proportions derived from physiological studies of N metabolism and excretion in cattle and wild ungulates (see Augustine and others 2003).

Finally, we used ion-exchange resin bags to obtain an additional index of inorganic N availability (Binkley 1984; Binkley and Hart 1989). Accumulation of inorganic N on the resin depends on inorganic N pool size, N mineralization rates, ion form ( $\text{NO}_3^-$  vs  $\text{NH}_4^+$ ), water movement to the bags, and competition for nutrients with microbes and plants (Binkley and Hart 1989). Although specific mechanisms controlling accumulation of N on the resin may be difficult to interpret, this method provides an index of overall inorganic N availability in the soil during an incubation period (Binkley and Hart 1989). Bags consisted of two approximately  $5 \times 4 \text{ cm}$  pieces of nylon sewn together and filled with two level tablespoons (29.6 ml) of mixed-bed ion-exchange resin (Dowex MR-3, a 1:1 mixture of HCRS[ $\text{H}^+$ ] and SBR[ $\text{OH}^-$ ]). Bags were buried by creating a 10-cm deep hole with a 12.5 cm dia soil auger, then excavating a space for the resin bag perpendicular to the auger hole at a

depth of 7–8 cm. We used 6 bags per glade per grazing treatment and 12 bags per bushland site per grazing treatment with bushland sampling stratified between and beneath shrubs. Bags were retrieved and new bags were buried in new locations every time aboveground biomass was measured during the first four measurement intervals (March–July) of 2001.

### Clipping vs. Grazing Experiment

A clipping experiment was conducted at three glades to compare ANPP and soil N dynamics under three treatments: (1) grassland where plants are defoliated by ungulate herbivores, and that plant matter is returned to the ecosystem as dung, urine and respired CO<sub>2</sub>, (2) grassland where plants are defoliated by clipping, but the plant matter does not pass through an ungulate digestive system and is instead returned to the soil surface as plant litter, and (3) grassland with no ungulate presence and no defoliation. When the large exclosures were built in 1999, three 2 × 2 m plots were randomly selected within each exclosure, and herbs on these plots were clipped to the same height as herbs on grazed plots at monthly intervals until August, 2001. Each time the plots were clipped, herb clippings were left in place on the soil surface. Thus, plants in these plots received the same level of defoliation as in the grazed plots, but clipped material was transferred directly to soil microbes, instead of through the digestive system of large herbivores and back to the soil as dung and urine. Productivity and soil N dynamics were measured during March–August in 2001, with the exception that ion-exchange resin bags were only used during the first two months (March–May). At the end of the study in August, biomass of the litter and dung layer was measured in grazed, clipped and fenced (ungrazed + unclipped) treatments using six 20 × 20 cm quadrats per treatment and site, and standing dead biomass was measured by canopy interception. Dung biomass on grazed plots was measured to provide an indication of the magnitude of dung inputs to the soil surface in this treatment, but we note that dung biomass on plots may have been derived from plants grown elsewhere.

### Statistical Analyses

Differences in ANPP and inorganic N dynamics between communities and grazing treatments were analyzed using split-plot ANOVAs (grazing treatment applied within communities) that also included a block (site) term. Data were log-trans-

formed as necessary to reduce heteroscedasticity. In cases where significant community × grazing interactions were detected (for interaction terms in the ANOVA,  $\alpha \leq 0.1$  was used as the threshold for potentially significant interactions; Stehman and Merideth 1995), then planned contrasts of grazing effects within each community were evaluated with a two-sided *t*-test using the mean squared error associated with the split-plot treatment (grazing) from the overall ANOVA (Keuhl 2000). Following convention, we used  $\alpha \leq 0.05$  as the threshold for tests of significance for all simple and main effects in the experiments. For the clipping study, variables were only measured for a single community, so one-way repeated measures ANOVAs were used and treatment means within each month were compared using the Waller-Duncan *k*-ratio with *k* = 100, which is equivalent to an experiment-wide error rate of 0.05.

## RESULTS

Glade soils were similar to bushland soils in terms of texture, but glade soils contained 2.0 times more total N than bushland soils between shrubs and 1.4 times more total N than bushland soils beneath shrubs (Table 1). Glade soils also contained 2.0 times more total C than bushland soils between shrubs, 1.3 times more total C than bushland soils beneath shrubs, and 8.6 times more total P than bushland soils (Table 1).

### Grazer Effects on Plant Dynamics

Grazer effects on herbaceous ANPP over the 3 years of study were contingent on both soil fertility and rainfall patterns. During the first year of the small-scale exclosure experiment, when rainfall was only slightly below average and occurred as a 2-month growing season in April–May plus a 1-month growing season in August, there was a significant interaction between the effects of grazing and site fertility (Figure 1A;  $F_{1,6} = 3.97$ ,  $P = 0.093$ ) because grazers had no effect on ANPP at glades ( $t_6 = 0.21$ ,  $P = 0.84$ ), but reduced ANPP by 29% at bushland sites ( $t_6 = 3.03$ ,  $P = 0.023$ ). Across all grazing treatments, glade productivity was significantly greater than bushland productivity ( $F_{1,3} = 14.71$ ,  $P = 0.031$ ).

In contrast, ANPP in 2000 was negatively affected by herbivores across all communities (community × grazing:  $F_{1,6} = 2.65$ ,  $P = 0.16$ ; grazing:  $F_{1,6} = 8.18$ ,  $P = 0.028$ ). Herbaceous production in 2000 primarily occurred during short but intense, mid-drought rains in August, and was 117%

**Table 1.** Soil Properties (mean, 95% CI in parentheses) of Glades and Bushland Study Sites at the Mpala Research Centre

	Glades	Bushland	
		Beneath shrubs	Between shrubs
Total soil N (%)	0.191 (0.056)	0.137 (0.029)	0.095 (0.019)
Total soil P (%)	0.133 (0.035)	0.016 (0.003)	0.015 (0.009)
Total soil C (%)	1.76 (0.65)	1.31 (0.33)	0.86 (0.20)
C:N ratio	9.2	9.6	9.1
N:P ratio	1.4	8.6	6.3
% Sand	75.3 (7.0)		74.3 (9.2)
% Clay	10.0 (2.3)		14.8 (3.3)

greater inside versus outside fences at bushland sites and 27% greater inside versus outside fences at glade sites (Figure 1B). Productivity was only marginally greater in glades compared to bushland sites ( $F_{1,3} = 6.70$ ,  $P = 0.081$ ).

Finally, for the large-exclosure experiment during 2001, a strong community  $\times$  grazer interaction was detected during the long, 5-month wet season ( $F_{2,6} = 12.05$ ,  $P = 0.008$ ). At one extreme, grazers increased productivity by 22% at glade sites (overcompensation,  $t_6 = 3.47$ ,  $P = 0.013$ ) whereas grazers reduced productivity by 68% (undercompensation;  $t_6 = 2.89$ ,  $P = 0.028$ ) in bushland communities between shrub canopies (Figure 1C). No effect of grazing on ANPP was detected for bunchgrass communities beneath shrub canopies ( $t_6 = 1.76$ ,  $P = 0.13$ ). Only a marginal difference in productivity was observed among communities ( $F_{2,4} = 4.57$ ,  $P = 0.093$ , Figure 1C).

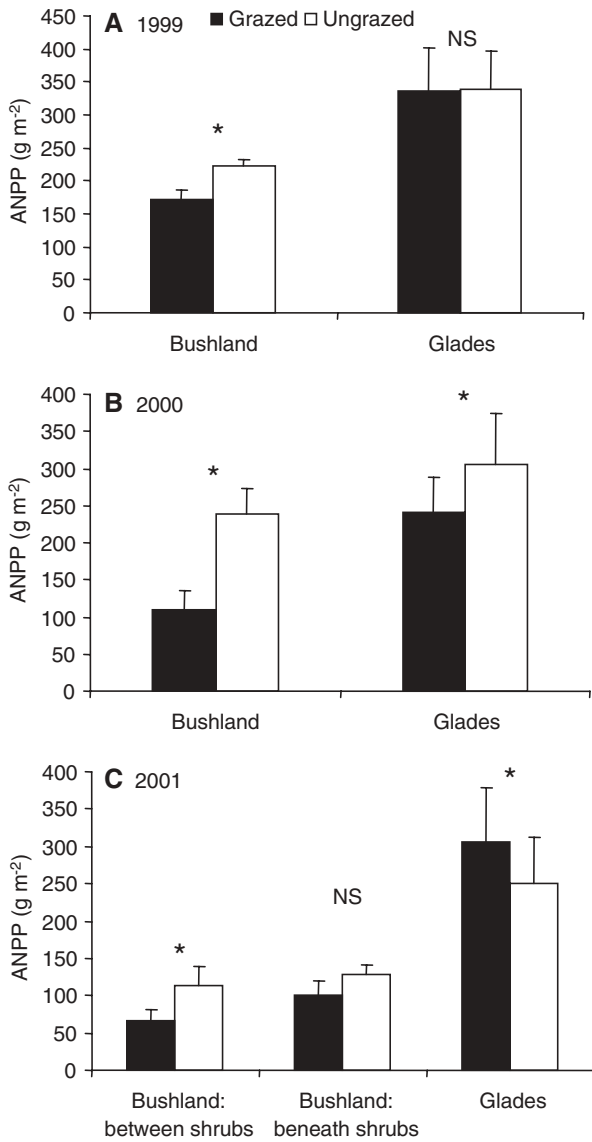
The negative effect of grazers on ANPP in 2000 (Figure 1B) was during a drought year when most production occurred in a 1-month growing season. In contrast, the positive effect of grazers on ANPP in glades during 2001 (Figure 1C) occurred in an above-average rainfall year over a 5-month growing season. To further examine whether the results from 2001 are comparable to the results from 2000, the temporal pattern of cumulative ANPP over the 5-month growing season in 2001 was analyzed (Figure 2). After the first month of the growing season in 2001, grazing reduced productivity across all communities (April ANPP; community  $\times$  grazing:  $F_{2,6} = 1.49$ ,  $P = 0.30$ ; grazing:  $F_{1,6} = 36.7$ ,  $P = 0.001$ ), consistent with the findings for the 1-month growing season in 2000. After a 2-month growing season in 2001, there was a significant grazing  $\times$  community interaction ( $F_{2,6} = 3.68$ ,  $P = 0.091$ ), and analyses of simple effects showed that ANPP was similar in grazed and ungrazed treatments on glades ( $t_6 = 1.02$ ,  $P = 0.35$ ) but was marginally reduced by grazers on bushland sites

(beneath shrubs:  $t_6 = 2.36$ ,  $P = 0.056$ ; between shrubs:  $t_6 = 2.30$ ,  $P = 0.061$ ). By the end of the full 5 month growing season, the grazer effect in glades was significantly positive ( $t_6 = 3.47$ ,  $P = 0.013$ ) whereas the grazer effect on bushland sites was significantly negative ( $t_6 = 2.89$ ,  $P = 0.028$ , Figure 2).

### Grazer Effects on Soil N Dynamics

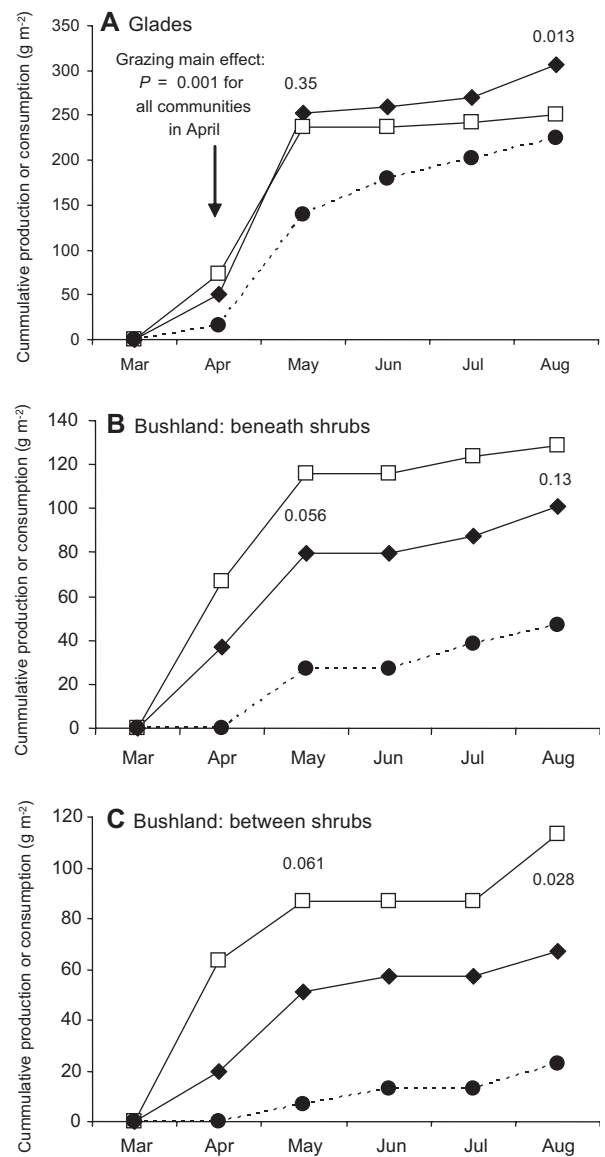
We examined effects of large herbivores on three measures of soil inorganic N availability and turnover: (1) extractable soil inorganic N concentrations, (2) N-mineralization rates, and (3) N-adsorption rates to ion-exchange resin bags. Due to the limited area available for destructive sampling in the small-exclosure experiment, only the first variable was measured in 2000. During the drought in May, 2000, soil inorganic N concentrations varied significantly in relation to both grazing and community (grazing  $\times$  community:  $F_{1,6} = 8.64$ ,  $P = 0.026$ ; grazing:  $F_{1,6} = 19.72$ ,  $P = 0.004$ ; community:  $F_{1,3} = 24.55$ ,  $P = 0.016$ ). Grazers increased extractable N concentrations at glades [grazed vs. ungrazed =  $33.3 \pm 4.9$  vs.  $13.2 \pm 2.1$  mg inorganic N kg dry soil<sup>-1</sup> ( $\bar{X} + 1$  SE);  $t_6 = 20.1$ ,  $P < 0.0001$ ] and at bushland sites (grazed vs. ungrazed =  $9.7 \pm 1.1$  vs.  $5.6 \pm 1.8$  mg inorganic N kg dry soil<sup>-1</sup>;  $t_6 = 4.1$ ,  $P = 0.006$ ). The community  $\times$  grazing interaction indicates the grazer effect was significantly larger in glades compared to bushland sites.

Soil inorganic N concentrations in 2001 varied significantly in relation to grazing, community, and time. Across all 6 months, no significant community  $\times$  grazing interactions were detected ( $F_{1,6} \leq 2.22$ ,  $P \geq 0.19$ ). In March 2001, prior to the onset of rains and following a long, severe dry season, grazers dramatically increased soil inorganic N concentrations in all communities (Figure 3). The magnitude of the grazer effect on soil inorganic N declined early in the growing season, and then



**Figure 1.** Effects of large herbivores on herbaceous aboveground net primary productivity (ANPP  $\text{g m}^{-2}$  summed over a 6 month study period in 1999 and 2000 and a 5 month study period in 2001) for glade and bushland communities at Mpala. Results are from a slightly below-average rainfall period in 1999 (A), a severe drought in 2000 (B), and an above-average rainfall year in 2001 (C). Asterisk indicates a significant difference between grazing treatments at the  $\alpha < 0.05$  level; NS denotes  $\alpha > 0.05$ . Error bars show  $+1$  SE based on among-block variation, while tests of statistical differences among communities and grazing treatments control for among-block variation.

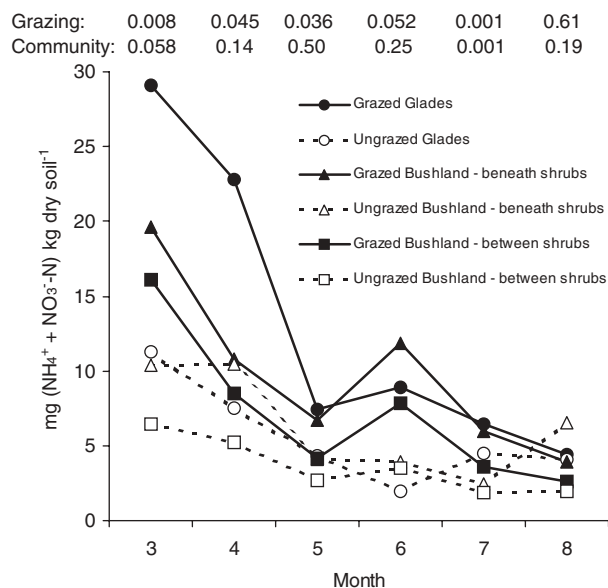
increased again after plants reached peak biomass (Figure 3). Following another period of plant growth during July and August, inorganic N declined and reached similar levels in grazed and ungrazed treatments by August (Figure 3). During



**Figure 2.** Temporal patterns of cumulative large-herbivore forage consumption (solid circles), cumulative ANPP in the presence of large herbivores (solid diamonds) and cumulative ANPP in the absence of large herbivores (open squares) over a 5-month growing season in 2001. In May and August, there was a significant grazer  $\times$  community interaction, so the  $P$ -values of the contrasts comparing grazed versus ungrazed ANPP in each community are reported above or between the points for each community. Grazers reduced ANPP throughout the growing season in between-shrub bushland communities, but the grazer effect switched from negative to positive in glades. Note differences in the scale of the  $y$ -axis in A, B and C.

the drought in 2000, the small-exclosure experiment showed that grazers increased soil inorganic N concentrations by 153% in glades and 72% in bushland communities. At the end of the drought in March of 2001, the large-exclosure





**Figure 3.** Variation in extractable soil inorganic N concentrations in relation to grazing and community type over a 6 month study season in 2001. *Solid lines and symbols* show monthly concentrations in grazed communities; *dashed lines and open symbols* show monthly concentrations for fenced communities. *Circles* show glades, *triangles* show bushland communities beneath shrub canopies and *squares* show bushland communities between shrub canopies. Above each month, the upper row of numbers shows *P*-values for the main effect of grazing and the lower row of numbers shows *P*-values for the main effect of community type.

experiment similarly showed that grazers increased inorganic N concentrations by 158% in glades and 89% in bushland communities (Figure 3).

In contrast to the consistently elevated soil inorganic N concentration in grazed treatments, grazers suppressed N mineralization rates early in the growing season, and had no detectable effect thereafter. Analysis of monthly patterns of N mineralization rates for the 5-month growing season in 2001 showed that during the first month of the growing season (April), grazers did significantly reduce N mineralization rates across all communities (community  $\times$  grazing interaction:  $F_{2,6} = 0.31$ ,  $P = 0.74$ ; grazing:  $F_{1,6} = 45.65$ ,  $P = 0.0005$ ). The magnitude of this effect was substantial, with a mean N mineralization rate in April of  $0.0 \pm 0.4$  g N  $m^{-2}$  month $^{-1}$  ( $\bar{X} \pm 1$  SE) in the presence of grazers, and  $1.5 \pm 0.6$  g N  $m^{-2}$  month $^{-1}$  in the absence of grazers. However, no significant grazer or community effects were detected during the remainder of the growing season (May–August). The size of the inorganic N pool that accumulated during the dry season was the primary contribution to N availability during the growing season (rather

than N-mineralization) in glades and in grazed bushland sites, but in ungrazed bushland sites, N-mineralization contributed more to N availability than the dry-season inorganic N pool (Table 2).

Finally, grazers differentially affected rates of inorganic N adsorption to ion-exchange resin bags in glade versus bushland communities (Figure 4). N-adsorption rates summed over the four measurement intervals from April to July were significantly reduced by grazers in bushland communities between shrub canopies, but significantly increased by grazers in glades (community  $\times$  grazing interaction:  $F_{2,6} = 35.4$ ,  $P < 0.001$ , Figure 4). Analyses of the monthly patterns showed the greatest differential effects occurred during the first month of the growing season in April (community  $\times$  grazing:  $F_{2,6} = 12.85$ ,  $P = 0.007$ ) and to a lesser degree in May (community  $\times$  grazing:  $F_{2,6} = 6.04$ ,  $P = 0.036$ ).

### Clipping Experiment

On glade plots that received the 2-year clipping treatment, ANPP ( $\bar{X} \pm 1$  SE =  $277 \pm 75$  g  $m^{-2}$ ) was intermediate between ANPP for grazed and fenced treatments (see Figure 1C). Aboveground dead biomass was similar on clipped and grazed plots, but consisted primarily of dung on grazed plots and plant litter on clipped plots. Despite the minimal differences in ANPP, there were statistically significant differences between grazed and clipped plots during the first 2 months of the growing season in terms of soil inorganic N content (Figure 5A), resin N-adsorption rates (Figure 5B) and N mineralization rates (Figure 5C). For all three of these soil variables, dynamics on clipped plots were statistically indistinguishable from fenced (ungrazed and unclipped) plots (Figure 5A–C).

## DISCUSSION

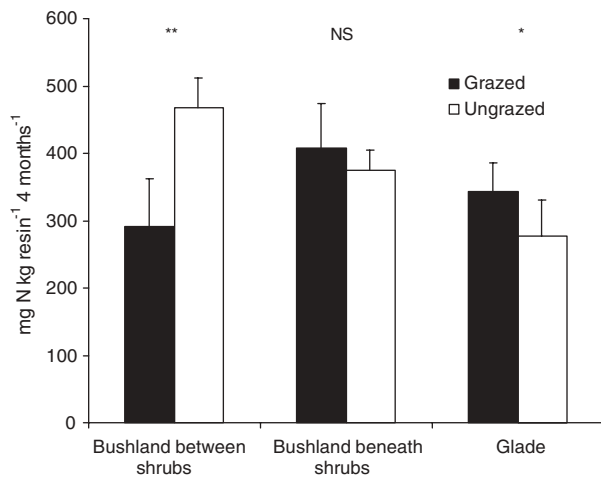
### Grass-Grazer Coupling in Semi-arid Ecosystems

Our results address two central issues in rangeland and ecosystem ecology. First, despite high annual variability in rainfall in Laikipia, large herbivores still strongly influence primary productivity and patterns of N cycling. In every year of the study, grazers reduced ANPP in nutrient-poor bushland communities. The greatest negative effects occurred during the short, mid-drought rains in 2000 and during the first month of the 2001 growing season, which followed the severe drought in 2000. These findings provide experimental evidence contradicting the view (Ellis and Swift 1988; Ellis

**Table 2.** Inorganic N Dynamics during the Primary Period of Plant Growth (March–May) in 2001

	Bushland					
	Glades		Beneath shrubs		Between shrubs	
	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed
Decline in inorganic N pool	4.52 (1.20)	1.46 (0.45)	2.93 (0.63)	1.43 (0.91)	2.69 (1.00)	0.85 (0.53)
N mineralization	-1.74 (0.42)	0.55 (0.68)	2.19 (0.63)	2.86 (0.91)	-0.30 (1.00)	2.39 (0.53)
Urine input	0.56 (0.06)	0.00	0.08 (0.03)	0.00	0.08 (0.03)	0.00

All values are in grams N m<sup>-2</sup> and numbers in parentheses show 1 SE.

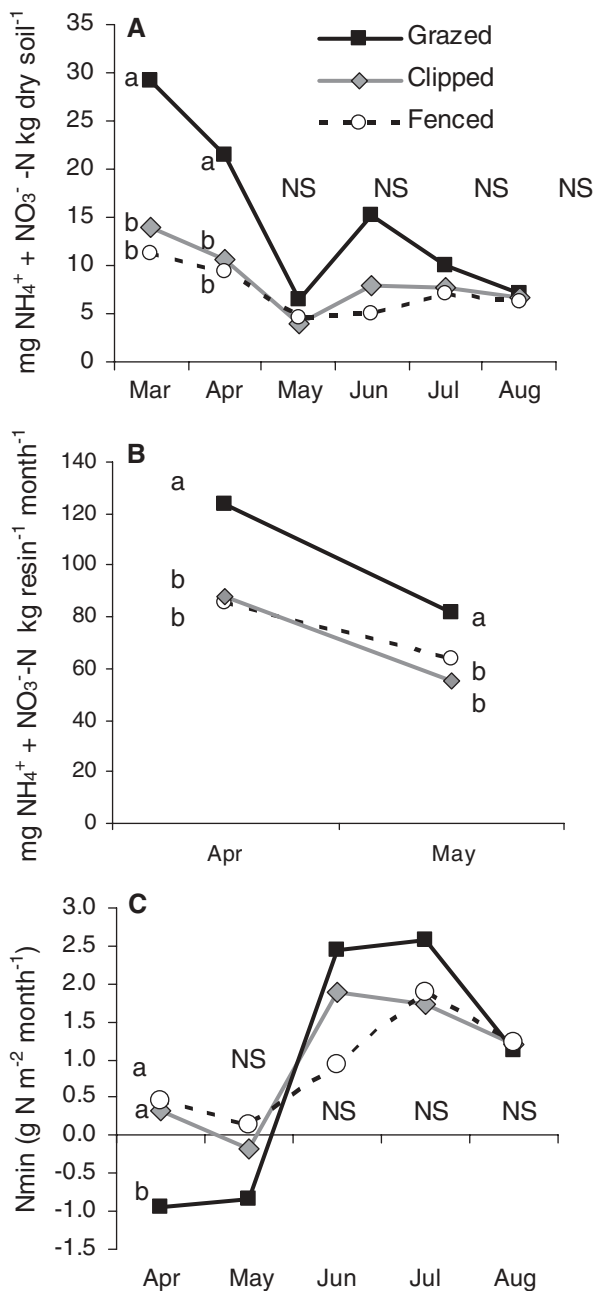


**Figure 4.** Inorganic N ( $\text{NH}_4^+ + \text{NO}_3^-$ ) adsorption to ion-exchange resin bags summed over 4 months for grazed and ungrazed communities at Mpala. Double asterisks indicate a significant difference at the  $P < 0.001$  level, single asterisk indicates a difference at the  $P < 0.05$  level, and NS indicates no significant difference. Error bars show +1 SE.

and others 1993) that herbivory has little impact on the dynamics of climatically variable systems. In particular, results support the hypothesis that “drought may impose intense and localized defoliation on vegetation, and this may result in ... loss of productive potential” (Illius and O’Connor 1999: 798). From November of 1998 until March of 2000, Mpala supported 14.7–16.5 cattle km<sup>-2</sup> (averaging 4685 kg km<sup>-2</sup>). Following the failure of the long rains during April–July in 2000, cattle mortality and sales only reduced density to 13.4 km<sup>-2</sup> so grazing on plants that grew during mid-drought rains was still intense. The major drought-related decline in cattle density (due to mortality and emigration) did not occur until after these brief mid-drought rains, with cattle reaching a low of 7.1 km<sup>-2</sup> in March 2001. Negative effects of grazers

on productivity during the first month of the growing season in 2001 were not due to intensive grazing in that month, but rather due to grazer effects in the previous drought year. This pattern again supports the argument that in climatically variable ecosystems, ungulate densities can increase in favorable years to levels that impose ecologically significant levels of defoliation on the plant community in low-rainfall years, thus making the ecosystem more prone to the effects of large herbivores (Illius and O’Connor 2000).

Second, herbivore effects on energy and nutrient fluxes were not always negative. Ecosystem responses were contingent on both rainfall and soil fertility. In every year of the study, ANPP of nutrient-rich glades was less negatively affected by grazers than ANPP of nutrient-poor bushland communities. Although a negative effect was found in all communities during the short growing season in 2000 (27% reduction in glades and 117% reduction in bushland sites), grazer effects switched from negative to positive in nutrient-rich sites during the 2001 growing season, thus providing empirical support for the nutrient-mediation hypothesis (Ritchie and others 1998; Bardgett and Wardle 2003). A switch in the direction of grazer effects was also documented in glades over the course of the growing season in 2001, suggesting that nutrient-rich, perennial grasslands can tolerate intensive, chronic grazing pressure only if adequate soil moisture is available for two or more consecutive months. Similar findings were reported by Biondini and Manske (1996) for temperate mixed-grass prairie, where grazing reduced ANPP in a drought year but had no negative effects in higher-rainfall years. Overall, our findings indicate that plant dynamics in semi-arid ecosystems are not a simple function of rainfall patterns or herbivory, but are regulated by the interactive effects of rainfall, grazing pressure and soil nutrients.



**Figure 5.** Comparisons of **A** soil inorganic N content, **B** N-adsorption to resin bags, and **C** N-mineralization rates for fenced, clipped and grazed plots at glade study sites at Mpala. Letters next to symbols indicate significant differences among treatments for any given month. NS denotes months with no significant differences among any treatments ( $P > 0.05$ ).

### Grazer Effects on Soil Nutrient Dynamics

Grazer effects on soil N occur at every temporal scale from months to years to decades in this ecosystem. Decadal effects occur due to cattle management, which generates spatial heterogeneity in

soil nutrients through bomas (typically 0.5–1.0 ha) that are distributed across the landscape and eventually develop into glades (Augustine 2003a). On an annual basis, herbivores influence the N budgets of different patches within the landscape. In glades, impala created a net N input due to high rates of dung and urine deposition during dry seasons when no forage is being consumed from these patches (Augustine and others 2003). In contrast, cattle cause a net loss of N from intensively grazed bushland patches because much of the consumed N is redistributed to bomas (Augustine and others 2003). On a monthly time scale, grazers also affected patterns of inorganic N availability (this study, Figures 3, 4). Monthly patterns of inorganic N availability should be interpreted in the context of grazing intensity and timing, the total soil N pools of the different communities, and the way herbivores affect long-term N balance. Theoretical analyses of soil-plant-herbivore interactions link these N dynamics across temporal scales by showing that transient (that is, short-term) grazer effects on ANPP depend on how grazers affect transient nutrient turnover rates, whereas long-term grazer effects on plant community stability ultimately depend on how grazers influence total soil nutrient pools (de Mazancourt and others 1998).

In this study, we used landscape-level variability in total soil C, N and P content induced by cattle bomas to assess how augmentation of soil nutrients over long time scales ( $> 40$  years) can influence short-term soil-herbivore interactions. We note that glades were enriched in total soil P (Table 1), and that adequate P availability is necessary for grasses to recover from defoliation (Chapin and McNaughton 1989). Soil P availability does interact with nitrogen to limit productivity in this ecosystem (Augustine and others 2003) and high P concentrations in glade grasses may be one important factor maintaining the stability of glade communities despite intensive grazing pressure (Chapin and McNaughton 1989).

Across all communities, grazers significantly increased soil inorganic N concentrations during dry seasons, this increase being even greater in glades than bushland communities. In contrast, grazers decreased N-mineralization rates in all communities during the first month of the growing season. Because the inorganic N pool that develops during dry seasons is the primary determinant of N availability to plants early in the growing season (Augustine and McNaughton 2004), our results suggest that the balance between positive grazer effects on dry-season inorganic N pools and nega-

tive grazer effects on N-mineralization early in the growing season ultimately controlled N availability during the growing season. Model simulations of soil N dynamics in the Serengeti grasslands of Tanzania draw similar conclusions about the combined importance of N-mineralization rates, inorganic N pools, and urine inputs as determinants of N availability in grazing ecosystems (Seagle and others 1992).

Findings in this study for N-mineralization are similar to those of Biondini and others (1998) for mixed-grass prairie in the USA, where intensive cattle grazing significantly reduced growing-season N-mineralization rates. In contrast, others have found that grazers increase N-mineralization rates on winter-range grasslands grazed by elk and bison (Frank and Groffman 1998) and in mixed-grass prairie grazed at moderate intensity by cattle (Shariff and others 1994), or had minimal effects in tropical grassland (Singh and others 1991; McNaughton and others 1997). In ecosystems where only moderate (~ 45%) amounts of ANPP was consumed, the increased N-mineralization rates combined with additional N recycled as urea may be an important factor facilitating grazer promotion of ANPP (Shariff 1993; Frank and McNaughton 1993). Negative grazer effects on growing-season N-mineralization (this study; Biondini and others 1998) may be a consequence of the large proportion of ANPP consumed by ungulates in both systems (60–90% of ANPP) consistent with the hypothesis that grazing intensity is one key determinant of how grazers affect mineralization (Biondini and others 1998).

Grazer-induced reductions in N mineralization may be linked to three types of effects on resource inputs to soils: (1) reduction in the quantity of resource inputs, resulting from reduced above- and/or below-ground plant production, (2) reduced quality of resource inputs, and (3) long-term changes in plant community composition (Bardgett and Wardle 2003). The second and third mechanisms are unlikely to have contributed to our results because ungulate grazers typically increase resource quality (by increasing nutrient concentrations in plant litter and returning organic matter to the soil as dung and urine rather than plant litter), and grazer effects on N-mineralization at Mpala were not associated with any changes in plant species composition. Grazer effects on root growth and turnover may be a more likely explanation. Although we did not measure grazer effects on root dynamics, root biomass is substantial; root measurements conducted at study sites during a dry month ( $\bar{X} \pm 1SE = 161 \pm 27 \text{ g m}^{-2}$  at glades

and  $136 \pm 12 \text{ g m}^{-2}$  at bushland sites, measured to a depth of 65 cm) were similar to peak above-ground biomass during the previous growing season ( $\bar{X} \pm 1SE = 126 \pm 25 \text{ g m}^{-2}$  at glades and  $166 \pm 31 \text{ g m}^{-2}$  at bushland sites; D. J. Augustine, unpublished data). Furthermore, the negative effect of grazers on N mineralization early in the growing season was not correlated with grazer effects on ANPP, again suggesting that N-mineralization dynamics may be more closely linked to grazer-induced reductions in the quantity of root inputs to the soil.

In grazing ecosystems, not all nitrogen is cycled via mineralization by soil microbes. An estimated 45–80% of all organic N consumed by ungulates is recycled as urea, with the largest amounts occurring in the growing season when forage N concentration and digestibility is greatest (Floate 1981; Scholefield and others 1991). Because urine deposition is not represented in measures of N-mineralization, intensive grazing can significantly reduce organic substrates available to microbes for mineralization without necessarily reducing N availability. Measures of cumulative N availability in this study, using ion-exchange resin bags, showed a significant positive grazer effect in nutrient-rich glades and a negative grazer effect in the nutrient-poor bushland. Our results suggest that grazing in the nutrient-rich glades may have increased inorganic N pool size during the dry season to a greater degree than grazing reduced N-mineralization rates early in the growing season. In contrast, grazing in the nutrient-poor bushland dramatically reduced N-mineralization rates while increasing dry-season inorganic N pool size to a lesser extent, which may have resulted in the net negative grazer effect on N availability as measured by the resin bags. Most ecosystem-level studies of how herbivores affect N cycling have focused on N-mineralization rates (for example, Pastor and others 1993; Shariff and others 1994; McNaughton and others 1997; Frank and Groffman 1998) while few have included grazer effects on inorganic N pool size and seasonal patterns of soil N availability (but see Seagle and others 1992). Studies that focus on both mineralization rates and fluctuations in inorganic N pool size in arid and semi-arid ecosystems may provide greater insight to how grazers affect N availability.

The clipping experiment conducted in glades shed further light on mechanisms underlying grazer effects on N cycling. It is often suggested that rapid recycling of plant nutrients via herbivore dung and urine is an important component of N cycling rates in grasslands, but we are unaware of

any previous field studies that have experimentally uncoupled the effects of defoliation from the effects of forage digestion and recycling by herbivores. We found that all measures of N availability (inorganic N pool size, mineralization rates, and N-adsorption to resin bags) were similar for ungrazed and clipped treatments, whereas the effects of clipping differed significantly from the effects of grazers. In other words, removing grazers (with fencing) while simultaneously maintaining high levels of plant defoliation (through clipping) did significantly alter patterns of N cycling and availability compared to the treatment with ungulate grazers, in just 2 years. These results indicate that grazers, rather than grazing, cause the observed changes in N cycling. In particular, the animal-related aspects of herbivory (consumption and chemical transformation of plant tissue by ungulate digestive systems plus trampling activity) appear to more strongly influence short-term soil N dynamics than simply plant defoliation and subsequent plant-soil interactions. These findings support the notion that large mammalian herbivores play dual roles as consumers and decomposers in terrestrial ecosystems.

Grazer effects on N cycling are particularly important because they can feed back to grazer effects on plant productivity and community resilience. Previous studies show nitrogen limits plant production at Mpala (Augustine and others 2003), and many other semi-arid savannas (Penning de Vries and others 1980; O'Connor 1985; Snyman 2002). In nutrient-rich glades, grazers do not drain the system of nitrogen and furthermore they increase seasonal availability of inorganic N. This is associated with grazer-induced increases in ANPP during years with adequate rainfall and with the persistence of glades as nutrient-rich lawns in the face of intensive grazing pressure. On nutrient-poor rangeland, grazers drain the system of nitrogen over long time scales, reduce seasonal N availability, and suppress herbaceous ANPP. Whether these short-term effects on bushland N availability and herbaceous ANPP extend to longer-term degradation of the bushland community is unclear. However, the presence of 5–10 m diameter patches of sealed, bare soil and low-biomass annual communities within the bushland landscape (Augustine 2003b) may be a long-term consequence of localized negative grazer effects on total soil N, seasonal inorganic N availability, and ANPP in areas that were previously dominated by perennial grasses (Schlesinger and others 1990; Rietkerk and others 1997).

Positive or neutral grazer effects on ANPP have been hypothesized to result not just from enhanced

nutrient availability, but also from many interacting mechanisms operating at scales from individual plants to entire ecosystems. These include plant physiological responses to defoliation, maintenance of the vegetation in an immature growth stage, competitive release due to canopy opening (McNaughton 1979, 1985) and grazer effects on belowground inputs of organic matter and rates of nutrient recycling (Bardgett and Wardle 2003). The clipping experiment showed that grazer-mediated decomposition of organic matter (that is, the consumption and digestion of plant matter by gut microbes, rather than plant defoliation alone) is an important factor increasing N availability. In addition, the physiological responses of grasses to defoliation and the maintenance of the vegetation in an immature growth stage are dependent on nitrogen supply (Wegener and Odasz 1997; Hamilton and others 1998). Overall, results from both this study and others (reviewed by Bardgett and Wardle 2003) indicate that grazer effects on ANPP and N cycling are closely coupled in their direction, magnitude and spatial extent in terrestrial ecosystems.

Finally, our findings also indicate that climatic variability is an important determinant of plant-herbivore interactions, with negative herbivore effects on ANPP in low-rainfall years regardless of soil nutrient availability. Grazing intensity also appears to play a role in soil N dynamics, with suppression of N mineralization rates where resident grazers remove more than 60% of ANPP (this study; Shariff and others 1994; Biondini and others 1998). At Mpala, most grazing is by resident impala and cattle, which exert a relatively continuous, chronic grazing pattern on the plant community. Under this chronic grazing regime, grazers only promoted productivity at high soil nutrient availability in a high-rainfall year, and only by 22%. In contrast, in ecosystems dominated by migratory herbivores that exert a pulsed grazing pattern, grazers can increase ANPP by 30–100% (Cargill and Jefferies 1984; McNaughton 1985; Frank and McNaughton 1993) suggesting that the temporal pattern of grazing can facilitate positive plant-herbivore interactions to an even greater degree than observed at Mpala.

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