

## FEEDBACKS BETWEEN SOIL NUTRIENTS AND LARGE HERBIVORES IN A MANAGED SAVANNA ECOSYSTEM

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**Abstract.** Small-scale fertilization experiments have shown that soil nutrients limit plant productivity in many semiarid grasslands and savannas, but linkages among nutrients, grasses, and grazers are rarely studied in an ecosystem context. We used hectare-scale heterogeneity in soil nutrients created by cattle management practices within a geologically homogeneous savanna to examine relationships among soil nitrogen and phosphorus, above-ground net primary production (ANPP), grass nutrient content, and a mixed community of native and domestic herbivores on central Kenyan rangeland. Increasing soil N and P content was consistently associated with increasing plant productivity and rainfall use efficiency in wet, dry, and drought years. A fertilization experiment and analyses of grass N:P ratios across sites indicated that N is the primary limiting nutrient on nutrient-rich glades, whereas N and P co-limit productivity on nutrient-poor bushland sites. Variation in ANPP among patches within the landscape was linearly correlated with consumption rates of large herbivores. Grazing pressure was consistently high (>60% of ANPP) at all but one site in a dry year (1999), and was greater in nutrient-rich glades ( $73 \pm 4\%$  of ANPP) than in nutrient-poor bushland sites ( $43 \pm 7\%$  of ANPP) in a wet year (2001). Grasses of nutrient-rich sites contained sufficient P concentrations to meet requirements for pregnant and lactating ungulates, whereas grasses in nutrient-poor swards were P deficient. Even though native and domestic herbivores selectively used and intensively grazed nutrient-rich sites, productivity on these sites remained high throughout the study. Analyses of nitrogen budgets for nutrient-rich and nutrient-poor sites showed that large herbivores themselves caused a net N input to the former and a net N loss from the latter. Thus, large herbivores not only respond to heterogeneity in soil and plant nutrients across the landscape, but also play a role in maintaining the N-enriched status of highly productive and intensively grazed sites.

**Key words:** *grazing ecosystems; grazing intensity; impala; Kenya; livestock; mineral nutrition; nitrogen; nutrient limitation; phosphorus; semiarid rangeland; wildlife management.*

### INTRODUCTION

Although low and variable rainfall clearly influences the structure and dynamics of semiarid rangelands (Ellis and Swift 1988), soil nutrients have also been recognized as an important determinant of plant productivity in many low-rainfall savannas (Keya 1973, Penning de Vries et al. 1980, Donaldson et al. 1984, O'Connor 1985, Snyman 2002) and, in turn, can regulate the distribution and abundance of large herbivores (McNaughton 1988, 1990, Ben-Shahar and Coe 1992, Seagle and McNaughton 1992). Soil N and P can both limit plant production at annual rainfall levels as low as 200 mm/yr in Sahelian grasslands (Penning de Vries et al. 1980), and nitrogen is widely reported as limiting to grass production in South African savannas (O'Connor 1985, Snyman 2002). Studies evaluating the role of nutrient limitation in semiarid ecosystems have focused primarily on ungrazed grassland under con-

trolled conditions, and ecosystem-level studies evaluating linkages between soil nutrients, grass production, and grazers are relatively limited (McNaughton et al. 1988). Surprisingly, intense debate concerning the stability and dynamics of African rangelands has focused almost entirely on climatic variation and has ignored the potential importance of soil nutrient limitations (Ellis and Swift 1988, Ellis et al. 1993, Illius and O'Connor 1999, 2000, Oba et al. 2000). Given that savanna ecosystems encompass ~65% of the African continent and most are used by humans for livestock production, greater understanding of the effects of nutrients on the productivity and stability of intensively grazed semiarid savannas is needed.

Intense grazing is a fundamental feature of many grassland and savanna ecosystems, which are capable of supporting substantially more herbivore biomass than other terrestrial habitats (Detling 1988, Huntly 1991, Frank et al. 1998). Large herbivores often track landscape patterns in grass productivity, resulting in a linear increase in grass consumption with production (Frank et al. 1998). Although improved soil fertility can increase grass production, it remains unclear whether increases in soil fertility simply translate into intensive grazing pressure with no increase in produc-

Manuscript received 27 August 2002; revised 28 January 2003; accepted 16 February 2003. Corresponding Editor: N. T. Hobbs.

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tivity, or result in both increased production and consumption. In some temperate and tropical grasslands, abundant native ungulates consume 40–65% of above-ground production (McNaughton 1985, Frank and McNaughton 1992); grazing intensities as high as 80–90% of above-ground production have been documented for an Indian savanna supporting free-ranging cattle (Pandey and Singh 1992) and a southern Kenyan grassland grazed by wildebeest (Andere 1981). However, few studies have quantified grazing pressure in savannas supporting mixed livestock and native ungulate communities, or have examined how grazing pressure, productivity, and soil fertility covary.

Because fertilization experiments are often conducted at limited spatial and temporal scales, it is difficult to evaluate the importance of nutrient limitations in grazed landscapes. Nutrients flowing from soils to grasses to grazers within several square meters in a single year may not be cycled back to the same plot, and feedbacks to soil nutrient availability within the temporal scale of a fertilization experiment may be extremely limited. In contrast, studies conducted at large spatial scales encompass not only variation in soil nutrients across geological gradients, but also significant variation in rainfall and soil physical properties (Bell 1982, Ruess and Seagle 1994). To overcome these limitations, we examined grass-layer productivity and grazing intensity within a climatically and geologically homogenous landscape in central Kenya where cattle management practices have created hectare-scale variation in soil nutrient content. Cattle are managed using traditional pastoral practices whereby they are contained overnight in brush-ringed corrals or “bomas,” where significant quantities of dung and urine accumulate. Bomas are subsequently abandoned and colonized by a unique plant community as the manure layer becomes mixed with mineral soil (Stelfox 1986, Reid et al. 1995, Young et al. 1995). Soil carbon and nutrient content declines during the first four decades after boma abandonment, but bomas >40 years old remain significantly nutrient enriched relative to surrounding bushland soils for an unknown time period (Augustine 2003a), possibly up to centuries (Blackmore et al. 1990).

Abandoned cattle bomas are a widespread component of African savannas (Stelfox 1986, Blackmore et al. 1990, Reid et al. 1995, Young et al. 1995) and are testimony to the major role that livestock management plays in the redistribution of organic matter and nutrients at the landscape scale (Augustine 2003a). In addition, both cattle and native ungulates could influence the long-term nutrient balance of any given sward due to differential rates of nutrient consumption vs. deposition in dung and urine. The balance between nutrient consumption and deposition has the potential to both stabilize swards where herbivores represent a net nutrient input due to high relative dung and urine deposition rates, and to degrade swards where herbivores

represent a net nutrient drain due to high relative forage consumption rates (de Mazancourt et al. 1998). For example, Blackmore et al. (1990) hypothesized that nutrient-enriched patches created by human settlements abandoned centuries ago are stabilized by net nutrient inputs to these sites from native and domestic herbivores. However, empirical studies only recently have begun to address the role that grazers may play in the redistribution of nutrients within landscapes (Pastor et al. 1998, Turner 1998, Augustine and Frank 2001).

We examined variation in soil nutrients, above-ground herbaceous production, and grazing intensity among three types of study sites: nutrient-poor *Acacia* bushland; long-term glades derived from cattle bomas abandoned >40 years ago; and extremely nutrient-rich bomas abandoned only 12–24 years ago. We also used a fertilization experiment and N:P ratios in plant tissues to evaluate the relative degree to which N vs. P limits grass productivity in this ecosystem. Studies, which encompassed a dry year in 1999, a severe drought in 2000, and an above-average rainfall year in 2001, enable us to evaluate how climatic variability interacts with soil fertility. Finally, to examine whether grazers redistribute nutrients at the landscape scale, we quantified the balance between ungulate N consumption vs. N deposition in dung and urine within study sites. Thus, we evaluated not only the degree to which soil nutrients regulate plant productivity and ungulate grazing pressure, but also the role that herbivores play in maintaining or degrading nutrient-enriched patches.

#### STUDY AREA

This research was conducted at the Mpala Research Centre and associated Mpala Ranch (MRC), which encompasses 190 km<sup>2</sup> of semiarid savanna within the Laikipia district of central Kenya (37°53' E, 0°17' N). The study area is underlain by well-drained, moderate to very deep, friable sandy loam soils developed from metamorphic basement rocks (Ahn and Geiger 1987). Annual mean rainfall for southern MRC during 1972–2000 was 508 mm (cv = 0.44). During this study, rainfall averaged 410 mm in 1999, 296 mm in 2000, and 658 mm in 2001. Topography consists of gently rolling hills and all study sites were located along ridgelines or upper hillslopes.

Young et al. (1995) previously described a two-phase mosaic at MRC consisting of long-term glades (shortgrass patches, typically 0.5–1 ha in size, lacking woody vegetation; 1% of the landscape) and *Acacia*-dominated bushland (99% of the landscape). Aerial photographs of MRC taken in 1961 and 1969 were used to differentiate between long-term glades, defined as shortgrass patches present since 1961, and old boma sites that were abandoned after 1969. Analyses of an abandoned-boma chronosequence showed that 12–24 year old bomas contain 6.5 times more N and 18.5 times more P than surrounding bushland soils, whereas long-term glades contain 1.6 times more N and 8.7 times

TABLE 1. Concentrations (means with  $\pm 1$  SE in parentheses) of 13 elements (percentage of dry mass) in soils from three types of study sites in Kenya.

Element	Bushland	Glades	Bomas
C	1.09 (0.10)	1.76 (0.20)	7.99 (1.65)
N	0.116 (0.009)	0.191 (0.018)	0.762 (0.168)
P	0.015 (0.002)	0.133 (0.035)	0.283 (0.057)
Ca	0.102 (0.018)	0.377 (0.075)	0.743 (0.086)
Mg	0.028 (0.003)	0.061 (0.011)	0.453 (0.082)
K	0.075 (0.008)	0.134 (0.019)	0.266 (0.052)
B	0.00017 (0.00002)	0.00031 (0.00005)	0.00138 (0.00032)
Cu	0.00019 (0.00002)	0.00024 (0.00001)	0.00053 (0.00012)
Fe	0.193 (0.015)	0.206 (0.009)	0.309 (0.019)
Co	0.0003 (0.00003)	0.0003 (0.00001)	0.0003 (0.00002)
Na	0.0073 (0.0010)	0.0050 (0.0003)	0.0056 (0.0008)
Al	0.427 (0.032)	0.375 (0.020)	0.437 (0.021)

Note: "Bomas" refer to cattle bomas (overnight cattle corrals) abandoned 12–24 years ago, and "glades" are cattle bomas abandoned >40 years ago.

more P than bushland soils (Table 1; see Augustine 2003a). Glades and old bomas are dominated by a short-statured sward of *Cynodon plectostachyus*, a grazing-tolerant, perennial stoloniferous grass (Georgiadis and McNaughton 1988), which at MRC is found almost exclusively on glade and boma soils. In contrast, the herbaceous layer of the surrounding bushland community contains a heterogeneous mosaic of bare soil and perennial grasses including *Cynodon dactylon*, *Digitaria milanijana*, *Pennisetum mezianum*, and *Pennisetum stramineum* (Augustine 2003b). Woody vegetation is dominated by *Acacia brevispica*, *Acacia mellifera*, and *Acacia etbaica* (Young et al. 1995).

MRC is currently managed for cattle production using traditional Maasai herding methods, and the borders of the property are not fenced. Over the past decade, ~2000–3000 cattle have been maintained at MRC, with peak numbers occurring after high-rainfall years in 1997 and 1998, and minimum numbers occurring after a severe drought in 2000. Stocking rates were relatively constant at 14–16 cattle/km<sup>2</sup> (43–50 kg/ha) for the period January 1999–May 2000, then declined to a low of 7.2 cattle/km<sup>2</sup> in April 2001 as a result of emigration and mortality during the drought. Stocking rates increased to 10.8 cattle/km<sup>2</sup> in May 2001 as cattle were returned to MRC and reached 13.5 cattle/km<sup>2</sup> in August, 2001 (K. Wreford-Smith, *personal communication*). The most common native ungulates were impala (*Aepyceros melampus*), zebra (*Equus burchellii*), waterbuck (*Kobus ellipsiprymnus*), buffalo (*Syncerus caffer*), and eland (*Taurotragus oryx*). Impala occurred at densities of ~20/km<sup>2</sup>, whereas densities of all other native ungulates were low (<1/km<sup>2</sup>; Augustine 2002). Scrub hares (*Lepus saxatilis*) were also common, but densities were not measured. Native predators included spotted hyaena (*Crocuta crocuta*), wild dogs (*Lycaon pictus*), lion (*Panthera leo*), and leopard (*Panthera pardus*).

#### METHODS

##### *Field measures of soil–grass–grazer feedbacks*

Herbaceous ANPP and ungulate consumption rates were measured using moveable grazing cages (Mc-

Naughton et al. 1996) during 1999 and 2000 at each of four bushland, glade, and boma study sites distributed across the central and southern regions of MRC. Bushland sites were all located ~200 m from a paired glade site, occurred at the same topographic position as the nearby glade, and were all dominated by *Cynodon dactylon* between shrub canopies. At each bushland site, we used six 1-m<sup>2</sup> cages and six 1-m<sup>2</sup> control (grazed) plots. Sampling was stratified, with three cages and controls between shrub canopies and three cages and controls beneath shrub canopies. Only shrubs with canopy architecture that permitted grazing beneath them were used in this study. Beneath-shrub plots were dominated by *Cynodon dactylon* at two sites, by *Cynodon* and *Digitaria milanijana* at one site, and by *Pennisetum mezianum*, *D. milanijana*, and *Cynodon* at the fourth site. Based on surveys of abandoned bomas throughout the study area and discussions with ranch employees, we also located four bomas abandoned 12–24 years ago that were distributed across the same region as the glade and bushland study sites. Four 1-m<sup>2</sup> control plots and four 1-m<sup>2</sup> grazing cages were monitored at each glade and boma site. Bomas abandoned 12–24 years ago were dominated by *Cynodon plectostachyus* and the annual forb *Gynandropsis gynandra*, whereas glades were dominated by *Cynodon plectostachyus* and the annual forb *Tribbalus terrestris*. Cage and control sample sizes used within each study site were a compromise with the need to replicate across study sites; sampling intensity was adequate, given low within-site heterogeneity in herbaceous biomass and the fact that if grazing occurred within a given month, it was typically intense. However, we note that low levels of grazing by just a few animals during a given month would not be detected by the cage method.

Live and standing dead biomass were measured in cages and control plots every 24–28 days early in the growing season, 28–30 days late in the growing season, and 30–45 days during dry seasons. Cages were moved to new randomly located positions for each measurement interval, and ANPP was calculated as the sum of

positive increases in live biomass inside cages for all measurement intervals where this increase was statistically significant at the  $\alpha = 0.1$  level. Consumption was calculated as the sum of positive differences between live biomass inside vs. outside cages for all intervals where this difference was significant at the  $\alpha = 0.1$  level, plus the sum of significant, positive differences in dead biomass inside vs. outside cages. Biomass was measured by canopy interception, with 49 pins/plot passed through the canopy at a 45° angle. The canopy interception method was calibrated with clipped plots for each of six groups: stoloniferous grasses, bunchgrasses, *Pennisetum mezianum*, thin-leaved grasses, forbs, and standing dead biomass (for regression equations, see Augustine 2003b). In 2001, production and consumption were only measured at three glade and three bushland sites, and we used 12 cages and 12 control plots at each bushland site (six beneath shrubs, six between shrubs) and six cages and six control plots at each glade. Bushland sites studied in 2001 were all dominated by stoloniferous grasses between shrubs (*Cynodon dactylon* at two sites; *Digitaria milaniana* at one site) and bunchgrasses beneath shrubs (*Enteropogon macrostachyus* at two sites and *Cymbopogon pospischilii* and *Themeda triandra* at one site).

In 1998–1999, the study encompassed two complete dry–wet cycles: a dry season during December–March, a wet season during March–May, a dry season during May–July, and a wet season during July–August. In 2000, the study encompassed an extremely dry period during March–July and a single, short wet season during August–September. In 2001, studies were initiated in March (the last month of a year-long drought) and continued through a 5-mo wet season from March to August. Rain gauges were maintained within 2 km of all study sites and were monitored weekly. Patterns of ungulate consumption were only analyzed for 1999 and 2001, which encompassed complete dry–wet cycles. Studies in 2000 were only used in analyses of plant production because ungulate consumption was not measured during the first month after the major plant growth pulse.

In 1999, we collected subsamples of herbaceous biomass (sorted into live and dead components) from 20 × 20 cm quadrats clipped to ground level from caged plots every time we measured biomass at the glade and bushland study sites. Samples were transported to Syracuse University, Syracuse, New York, USA for determination of plant N content. Subsamples were also collected from all sites at peak biomass in all three years and were transported to Syracuse University for determination of plant N and P. Soil cores (0–15 cm depth, 5 cm diameter) were collected from each site (four per glade and boma site and eight per bushland site in 1999; six per glade and 12 per bushland site in 2001) and a subsample from each core was oven-dried and transported to Syracuse University. Total N and C

content of soils and plant tissues were analyzed by Dumas combustion with a Carlo-Erba CN Analyzer (Carlo-Erba, Milan, Italy). Concentrations of 10 nutrients (P, Ca, Mg, K, B, Cu, Fe, Co, Na, and Al) in soil and plant samples were analyzed by inductively coupled plasma spectroscopy (Leman Labs PS3000, Hudson, Massachusetts, USA) in simultaneous mode using sample preparation procedures described by McNaughton (1988). Water-holding capacity of soil cores was determined for a 25-g subsample by adding 25 mL water and recording the percentage drained by gravity after 30 min.

Dung deposition rates were measured on eight permanent 20-m transects at all glade and bushland sites during the 1998–1999 study season. Dung groups for each mammalian herbivore species were counted and cleared at every measurement interval concurrently with grass biomass measures. We used 20 × 1 m transects for impala, 10 × 0.5 m transects for scrub hares, and 20 × 2 m transects for all ungulates other than impala. For each species, 20–50 fresh dung groups were collected, dried, and weighed, and subsamples were transported to Syracuse University for determination of total N content to calculate dung deposition rates in grams of N per square meter per measurement interval for each species. Because estimates of production and ungulate consumption at bushland sites did not include the shrub layer, dung deposition by elephant, dik-dik, and giraffe (pure browsers) was excluded from the analysis. Impala dung groups decomposed rapidly early in the growing season when dung beetles were most active, so some groups were missed in April and August counts. Based on 30 fresh impala dung groups monitored weekly during the first month of the growing season, we derived a correction factor for the proportion missed over the entire month following the method of Plumptre and Harris (1995). Dung groups of other species were not observed to disappear completely due to dung beetle activity; hence, no correction factor was applied.

Urine deposition at each site was calculated from dung deposition rates for each species, following the method of Frank et al. (1994). Ratios of N excretion in dung vs. urine for each species were estimated from laboratory studies of N balance in ungulate herbivores. We used the general equation derived by Scholefield et al. (1991) for cattle, which gives a urine:dung N excretion ratio of 0.82 for a diet containing 1.5% N (used for dry-season months) and a urine:dung ratio of 1.94 for a diet containing 3% N (used for wet-season months). For impala, we used a dry-season urine:dung ratio of 1.0 and a wet-season ratio of 2.5, based on studies of white-tailed deer, *Odocoileus virginianus* (Holter et al. 1979), which are similar to impala in body size and diet. Similar ratios have also been reported for elk and peccaries (Mould and Robbins 1981, Carl and Brown 1985). For the nonruminants (zebras and scrub hares), we used a dry-season ratio of 1.2 and a



wet-season ratio of 2.1, derived from studies of horses, ponies, and donkeys (Reitnour and Treece 1970, Slade et al. 1970, Hintz and Schryver 1972, Izraely et al. 1989). For waterbuck and eland, which contributed <6% of total dung deposition, we used the same ratios as for cattle.

Clearly, estimates of N deposition in urine are sensitive to seasonal fluctuations in forage quality, and this ratio is not a fixed constant for any species. However, this ratio is not likely to vary among bushland and glade study sites, because the same animals move between the bushland and glades on a daily basis. In addition, there were abrupt seasonal transitions in forage quality during the 8-mo study period, with two pulses of rapid grass growth following intensive rains and an ~2-wk transition from wet to dry season following the cessation of rains. As a result, our use of wet- and dry-season ratios in different months reflects these abrupt changes in the availability of green forage. In addition, across all of the studies on cattle, equid, deer, and peccary N metabolism previously cited, the relationship between diet quality (percentage of N content) and urine : dung N excretion ratios is very similar, despite wide variation in body size and digestive strategies among these species. We also note that wet-season urine deposition estimates in this study are probably conservative because higher urine : dung N excretion ratios of 2.85–3.48 have been reported for cattle, elk, and peccaries consuming high-quality diets with N concentrations similar to those of glade and boma grasses at MRC (Mould and Robbins 1981, Carl and Brown 1985, Bussink 1994, Frank et al. 1994).

For each glade and bushland site, we compared estimates of N consumption over the 1998–1999 study period to estimates of N deposition in urine and dung to examine the effect of herbivores on the nitrogen balance of nutrient-rich glades and nutrient-poor bushland. Ammonia volatilization losses were estimated as 25% of urine deposition, based on studies in Tanzanian grassland with soil texture and pH similar to that of MRC (Ruess and McNaughton 1988). N deposition in rainfall was estimated from measures of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  in rainfall samples collected monthly during the 1998–1999 study season.

#### *N vs. P limitation of herbaceous production*

To further examine nutrient limitations to plant growth, we conducted a factorial N  $\times$  P fertilization experiment on a sward dominated by *Cynodon plectostachyus*, *Portulaca oleracea*, *Tribbalus terrestris*, and *Sporobolus pellucida*. The site was selected because herbaceous biomass and species composition were homogenous and the site's proximity to human habitations prevented any grazing by large herbivores during the study period. The only ungulates observed near study plots during the experimental period were dik-diks (*Madoqua kirkii*), which are browsers. No ev-

idence of grazing was observed in any plots during data collection.

The experiment was conducted in a randomized block design, with four blocks arranged from upper to lower hill slope. Within each block, four 2  $\times$  2 m plots were randomly assigned to treatments consisting of no fertilizer, N fertilization only, P fertilization only, and N + P fertilization. Fertilization consisted of 40 g N/m<sup>2</sup> applied as urea and/or 10 g P/m<sup>2</sup> applied as triple super phosphate. The experiment was initiated 20 days after the onset of the growing season, and biomass was measured by canopy interception on day 0, when fertilizer was applied, and again 18 days later. A 20  $\times$  20 cm subsample from each plot was also clipped to ground level on day 18; plant tissue was air dried and transported to Syracuse University for nutrient analyses. Plots were irrigated with the equivalent of 15 mm rainfall applied in three equal 5-mm events on day 0, day 5, and day 10 due to initial uncertainty as to whether rain would occur during the experiment. An additional 62 mm of natural rainfall occurred during days 4–12, and no further irrigation was applied. One 5 cm diameter  $\times$  15 cm deep soil core was collected from each plot prior to fertilization, and a subsample was transported to Syracuse University for total soil N and P determination.

We also analyzed N:P ratios in soils and herb biomass from bushland, glade, and boma sites, and within the fertilization experiment. We examined N:P ratios in the youngest, fully expanded leaves of *Cynodon* spp. (*C. dactylon* from bushland sites; *C. plectostachyus* from boma and glade sites). We collected 20 leaves, each from a different tiller, from four 1-m<sup>2</sup> plots at each site after a 1-mo growing season in August 1999. We also examined N:P ratios in live aboveground herbaceous biomass harvested at peak biomass in September 2000 and May 2001. These latter data sets included greater variation in species and stem content among and within sites relative to the analysis of leaf blades from *Cynodon* spp.

#### *Statistical analyses*

Relationships for ANPP vs. rainfall and for rainfall use efficiency (RUE) vs. soil N and P were evaluated with simple and multiple linear regression. Because the ratio of maximum/minimum rainfall and total soil N was greater than 5, we used logarithmic transformations of rainfall and soil N prior to analysis (Weisberg 1985). We followed the method of Weisberg (1985: 179–183) to test for differences in the slopes and intercepts of regressions among years and types of study sites. Fertilization effects were tested with a 2  $\times$  2 factorial ANOVA and the Waller-Duncan *K*-ratio was used to compare treatment means. Note that all reported means in this paper are means of replicate study sites within a given site category, and all reported standard errors reflect variation among the replicate study sites, not within-site variation.

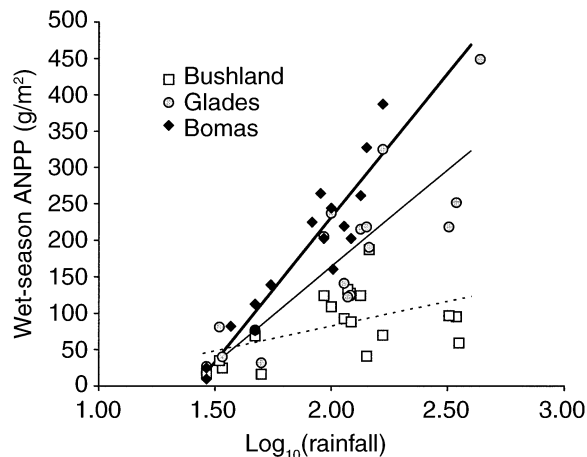


FIG. 1. Aboveground net primary production (ANPP) in the herbaceous layer as a function of rainfall for bushland, glades (>40-year-old abandoned bomas), and 12–24-yr-old abandoned bomas at the Mpala Research Centre, Kenya (MRC). Each point represents mean production of subplots within a given study site summed over a complete wet season.

## RESULTS

### *Productivity in relation to soil nutrients*

The relationship between rainfall and herbaceous production differed significantly among bushland, glade, and boma communities (Fig. 1). A regression model including different slopes and intercepts for each community explained significantly more variation in productivity than did the simplest model incorporating rainfall only ( $F$  test for comparison of models,  $F_{4,46} = 23.4$ ,  $P < 0.00001$ ) and significantly more variation than a model differentiating only between bushland vs. glades and bomas ( $F_{2,46} = 7.87$ ,  $P = 0.0011$ ). Production was only weakly related to rainfall in the bushland community ( $\text{ANPP} = 68.40 \times \log(\text{rainfall}) - 54.52$ ;  $r^2 = 0.24$ ,  $P = 0.038$ ), showed a far greater increase with rainfall in glades ( $\text{ANPP} = 265.40 \times \log(\text{rainfall}) - 367.20$ ;  $r^2 = 0.71$ ,  $P < 0.00001$ ), and an even greater rate of increase in bomas ( $\text{ANPP} = 395.51 \times \log(\text{rainfall}) - 559.86$ ;  $r^2 = 0.87$ ,  $P < 0.00001$ ).

Rainfall use efficiency (RUE, grams of aboveground herbaceous production per square meter per millimeter of rainfall) was positively correlated with total soil N content for the three seasons when rainfall across all sites was >50 mm (March–May 1999, July–September 2000, and March–August 2001; Fig. 2). A regression model including different slopes and intercepts for each year did not explain more variation in RUE than did a model including only different intercepts ( $F$  test for comparison of models,  $F_{2,24} = 2.28$ ,  $P = 0.124$ ), but intercepts varied significantly among years ( $F_{2,26} = 5.295$ ,  $P = 0.012$ ). Further analyses of differences among years showed that only the intercept for 2001 ( $\text{RUE} = 1.741 \times \log(\text{soil N}) + 2.038$ ;  $r^2 = 0.87$ ) differed significantly from the intercept for 1999 and 2000 ( $\text{RUE} = 1.487 \times \log(\text{soil N}) + 2.346$ ;  $r^2 = 0.63$ ;  $F$

test comparing a model differentiating among all three years vs. a model differentiating only between 2001 vs. 1999 and 2000,  $F_{1,26} = 2.15$ ,  $P = 0.15$ ). These results show that RUE was lower during the 5-mo growing season in 2001, a wet year, compared to RUE during shorter 1–2 mo growing seasons in 1999 and 2000.

Variation in productivity and RUE across communities could also be related to soil P, which covaries with soil N. Soil P explained a degree of variation in RUE ( $r^2 = 0.57$  for regression of RUE vs.  $\log_{10}[\text{total soil P}]$  for 1999–2000) similar to that of soil N ( $r^2 = 0.63$  for regression of RUE vs.  $\log_{10}[\text{total soil N}]$ ). In fact, nearly all soil nutrients covaried and increased from bushland to glade to boma study sites (Tables 1 and 2). Water-holding capacity did not differ for soils from glade vs. bushland sites ( $42.6 \pm 0.6\%$  and  $43.0 \pm 2.1\%$ , respectively,  $\bar{X} \pm 1 \text{ SE}$ ), but was significantly greater for bomas ( $53.7 \pm 2.6\%$ ), reflecting the high organic matter content of boma soils. To further evaluate the importance of N vs. P in limiting plant production, we evaluated N:P ratios in plant tissue from these communities and conducted a factorial N  $\times$  P fertilization experiment.

### *N vs. P limitation of herbaceous production*

Fertilization strongly affected herbaceous productivity ( $F_{6,9} = 8.63$ ,  $P = 0.003$ ), with a significant N  $\times$  P interaction ( $F_{1,9} = 6.33$ ,  $P = 0.033$ ). Addition of N alone increased productivity from  $7.2$  to  $9.6 \text{ g m}^{-2} \text{ d}^{-1}$ , P fertilization alone had no effect, whereas application of N and P together nearly doubled productivity (Fig. 3).

Across the bushland–boma chronosequence, soil N:P ratios (expressed on a mass basis) varied from 1.1–3.8 in glades and bomas to 3.5–11.5 at bushland sites.

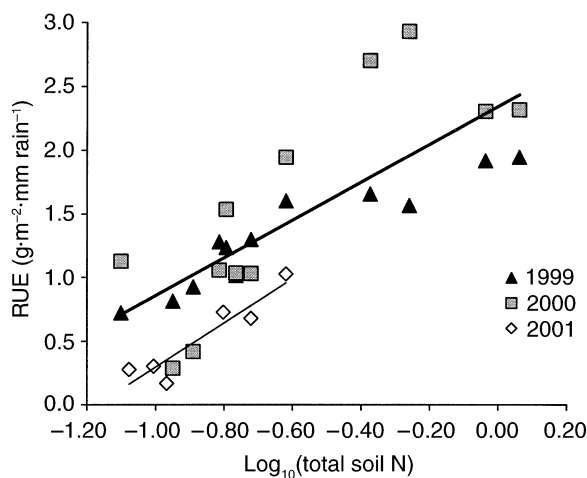


FIG. 2. Rainfall use efficiency (RUE) as a function of total soil N content (percentage dry mass) across study sites and years. The intercept of this relationship was significantly lower during a 5-mo growing season in 2001 compared to 1–2 month growing seasons in 1999 and 2000 (see Results).

TABLE 2. Correlation coefficients (*r*) for variation in total soil carbon and 12 mineral elements among bushland, glade, and boma study sites.

Element	N	P	K	Ca	Mg	B	Cu	Fe	Co	Na	Al
C	<b>1.00</b>	<b>0.8</b>	<b>0.89</b>	<b>0.88</b>	<b>0.96</b>	<b>0.98</b>	<b>0.95</b>	<b>0.8</b>	0.24	-0.06	0.12
N		<b>0.8</b>	<b>0.88</b>	<b>0.87</b>	<b>0.95</b>	<b>0.98</b>	<b>0.95</b>	<b>0.8</b>	0.23	-0.07	0.11
P			<b>0.93</b>	<b>0.98</b>	<b>0.92</b>	<b>0.90</b>	<b>0.86</b>	<b>0.8</b>	0.17	-0.21	0.02
K				<b>0.91</b>	<b>0.93</b>	<b>0.94</b>	<b>0.91</b>	<b>0.8</b>	0.13	-0.06	0.12
Ca					<b>0.91</b>	<b>0.89</b>	<b>0.83</b>	<b>0.8</b>	0.19	-0.22	0.07
Mg						<b>0.97</b>	<b>0.93</b>	<b>0.8</b>	0.23	-0.08	0.15
B							<b>0.97</b>	<b>0.8</b>	0.22	-0.01	0.12
Cu								<b>0.7</b>	0.13	-0.05	-0.03
Fe									0.35	-0.02	0.40
Co										<b>0.53</b>	0.43
Na											0.11

Note: Correlations that are significant at the  $P < 0.05$  level are shown in boldface.

N:P ratios were significantly greater in *Cynodon* leaf blades from bushland ( $\bar{X} = 13.5$ ) vs. glade and boma sites ( $\bar{X} = 10.2$ ;  $t_{10} = 3.32$ ,  $P = 0.0077$ ). Similarly large differences among sites were observed for above-ground herbaceous biomass N:P ratios in 2000 (bushland,  $\bar{X} = 14.6$ ; glades and bomas,  $\bar{X} = 8.3$ ;  $t_{14} = 11.75$ ,  $P < 0.001$ ) and 2001 (bushland,  $\bar{X} = 14.1$ ; glades and bomas,  $\bar{X} = 6.2$ ;  $t_7 = 6.43$ ,  $P < 0.001$ ). Soil N:P ratios were significantly correlated with *Cynodon* leaf N:P ratios (Fig. 4a;  $r = 0.69$ ,  $P < 0.05$ ) and herbaceous biomass N:P ratios (Fig. 4b;  $r = 0.76$ ,  $P < 0.05$ ).

Soils from the site of the fertilization experiment were similar in color and texture to bushland soils, contained C (1.15%) and N (0.13%) levels similar to those of bushland sites, but contained high levels of P (0.073%). As a result, soil N:P ratios were similar to those observed in glade and boma soils and plant N:P ratios were correspondingly low (Fig. 4b). N fertilization significantly increased N:P ratios in herbaceous biomass from 5.2 to 8.0 (Fig. 4b;  $F_{1,11} = 16.2$ ,  $P = 0.002$ ). P fertilization had no effect on N:P ratios ( $F_{1,11}$

$= 0.65$ ,  $P = 0.44$ ) despite the significant interactive effect of N and P on productivity.

*Ungulate consumption in relation to sward productivity*

Large herbivores tracked hectare-scale variation in grass production and nutrient content. Across sites, unguulate consumption rates increased linearly with ANPP (Fig. 5;  $r^2 = 0.94$ , consumption =  $0.8091 \times$  production - 30.68,  $F_{1,16} = 115.43$ ,  $P < 0.0001$ ). The slope of this relationship was nearly identical to the slope observed in the Serengeti and Yellowstone ecosystems (Frank et al. 1998), but the intercept for MRC was significantly greater than the intercept for Yellowstone and Serengeti ( $t_{55} = 2.063$ ,  $P = 0.044$ ; Fig. 5). Contrary to our original hypothesis, the percentage of herbaceous ANPP grazed was relatively constant across study sites in 1999. At all sites (except one ungrazed bushland site), >60% of ANPP was grazed, regardless of plant nutrient content. In 2001, the percentage of herbaceous ANPP grazed was significantly greater in glades ( $73 \pm 4\%$ ; mean  $\pm 1$  SE) compared to bushland sites ( $43 \pm 7\%$ ).

*Nitrogen redistribution via herbivores*

In glades, unguulate deposition of N in dung and urine ( $9.1 \pm 1.1$  g N/m<sup>2</sup>) exceeded total N consumed in forage ( $6.4 \pm 1.9$  g N/m<sup>2</sup>) by 43% over the 1998–1999 study season (Table 3; paired  $t_3 = 2.93$ ,  $P = 0.060$ ). However, deposition and consumption were similar during wet-season months ( $5.8 \pm 2.0$  vs.  $5.9 \pm 1.1$  g N/m<sup>2</sup>; paired  $t_3 = 0.11$ ,  $P = 0.92$ ). The net N input was due to high rates of dung and urine deposition during dry seasons ( $3.2 \pm 0.4$  g N/m<sup>2</sup>) when minimal consumption occurred ( $0.6 \pm 0.2$  g N/m<sup>2</sup>;  $t_3$  for dry-season consumption vs. deposition = 7.52,  $P = 0.005$ ). Impala were responsible for 72% of overall dung and urine inputs, and 78% of dry-season N inputs. Even after estimates of N losses via ammonia volatilization from urine patches and N deposition in rainfall are incorporated into the N budget (Table 3), ungulates have a net positive effect on the N balance at three of the four glade

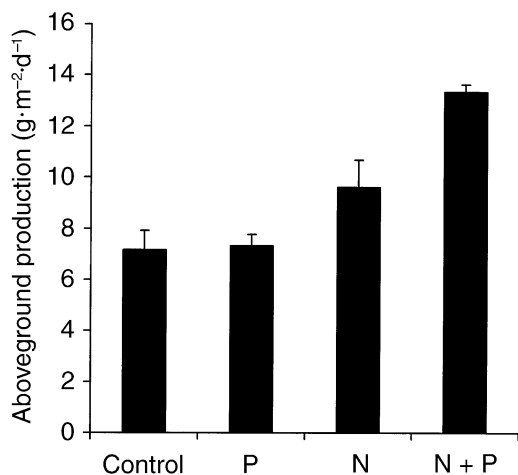


FIG. 3. Effects of fertilization on aboveground herbaceous production (mean + 1 SE) during the mid-wet season in 2001 at MRC, Kenya.

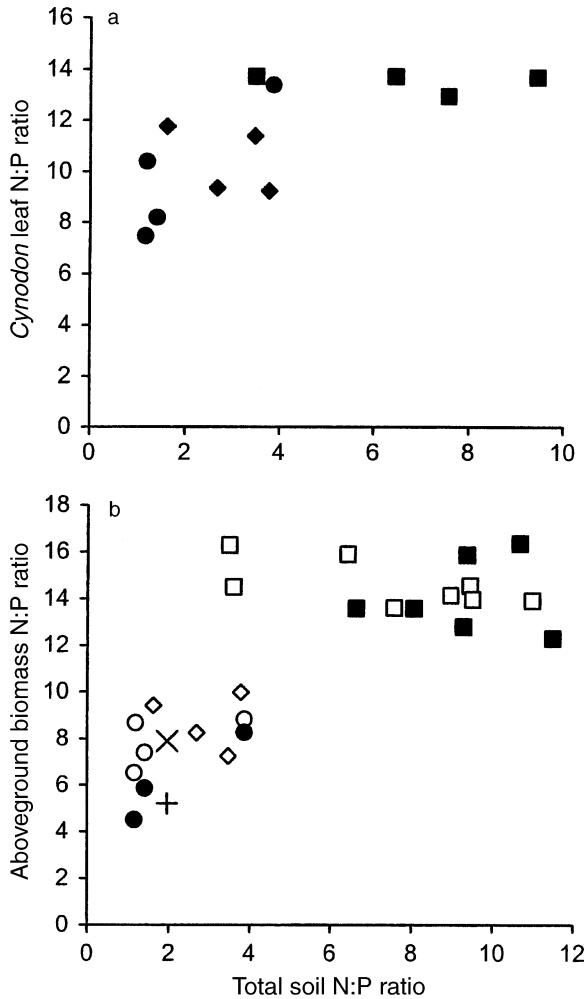


FIG. 4. Variation in soil and plant N:P ratios among bushland, glade, and boma study sites. (a) Variation in N:P ratios of *Cynodon dactylon* leaf blades from bushland sites (squares), and *C. plectostachyus* leaf blades from glades (circles) and bomas (diamonds). (b) Variation in N:P ratios for total aboveground herbaceous biomass in 2000 (open symbols) and 2001 (closed symbols); N:P ratios for plants from the fertilization experiment are also shown for plots receiving N fertilizer (×) and plots without N fertilizer (+).

sites. In contrast, N in forage consumed from nutrient-poor bushland sites exceeded N in dung and urine deposition by 1.4–1.5 g N/m<sup>2</sup> at each of the three sites where consumption occurred, giving a net N loss of 1.3–1.4 g N/m<sup>2</sup> after correcting for volatilization and rainfall (Table 3).

#### DISCUSSION

Short-term experiments at the plot scale have documented the widespread importance of N and P limitations on grassland productivity in Africa (Keya 1973, Penning de Vries et al. 1980, O'Connor 1985, Snyman 2002). Our findings extend this work by demonstrating increased productivity with increasing soil N and P in an ecosystem experiencing intensive, year-round graz-

ing by native and domestic ungulates (Figs. 1 and 2). Cattle, zebra, eland, and impala all used glades and bomas to a greater degree than expected based on their availability within the landscape, most likely in response to forage quality for cattle, zebra, and eland, and in response to both high forage quality and low predation risk for impala (Augustine 2002). Preferential use of glades and bomas was reflected in far greater absolute consumption rates on the more productive glade and boma swards, which, in turn, were closely correlated with ANPP (Fig. 5). Ungulate selection of productive patches within the landscape could be related to both energetic and nutrient-related aspects of forage quality (McNaughton 1988, Wilmhurst et al. 2000) because glade and boma swards were both enriched in N and P and contained higher leaf : stem ratios than bushland swards (Augustine 2002). Despite the resulting intense grazing pressure on glades, productivity on these sites remained high throughout the study. Furthermore, greater productivity on nutrient-rich vs. nutrient-poor sites occurred during a short, mid-drought rainy season (2000), a relatively dry year encompassing two 1–2 month wet seasons (1998–1999), and an above-average, 5-month wet season (2001; Fig. 2), emphasizing the importance of soil nutrients even in semiarid ecosystems characterized by large annual fluctuations in rainfall. Low RUE across all sites in the wet year of 2001 (Fig. 2) could be related

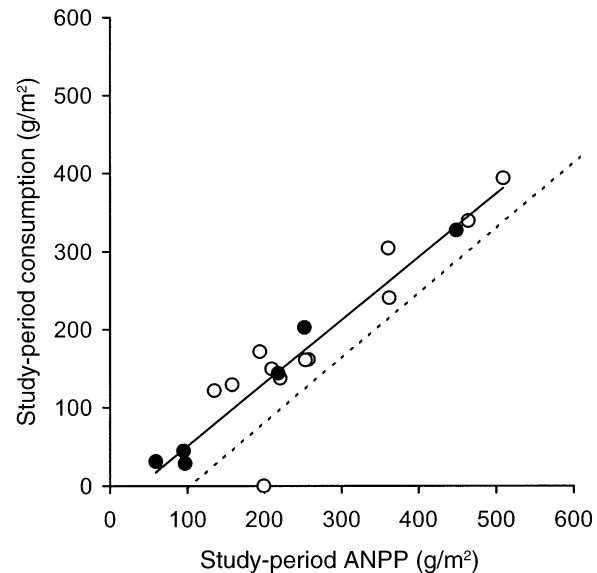


FIG. 5. Relationship between ANPP and large herbivore consumption rates for a 6-mo study period in 1999 (open circles) and a 5-mo study period in 2001 (solid circles) at MRC. Variation in ANPP among sites within a year was primarily related to variation in soil nutrient availability (Fig. 2). The solid line shows the regression for Mpala ( $r^2 = 0.94$ , consumption =  $0.8091 \times \text{ANPP} - 30.68$ ;  $F_{1,16} = 115.43$ ,  $P < 0.0001$ ). The dashed line shows the reported relationship for Yellowstone and Serengeti National Parks (Frank et al. 1998).



TABLE 3. Nitrogen fluxes at four glade and four bushland study sites summed over two wet–dry cycles spanning eight months during 1998–1999. Unless otherwise noted, values are in g N/m<sup>2</sup>.

Site	Deposition		Impala N input (%)	Total herbivore N deposition	N in rainfall	N consumed	Ammonia volatilized	Ungulate deposition minus consumption	Overall net herbivore effect†	Herbivore N deposition in dry season (%)
	Dung	Urine								
Glades										
1	3.8	7.5	81	11.3	0.25	9.0	1.9	2.4	0.8	22
2	4.1	6.5	70	10.6	0.25	10.3	1.6	0.3	-1.1	41
3	3.1	4.9	70	8.0	0.25	3.8	1.2	4.2	3.3	41
4	2.3	4.1	68	6.5	0.25	2.3	1.0	4.1	3.3	41
Mean	3.3	5.8	72	9.1	0.25	6.3	1.4	2.8	1.6	36
Bushland										
1	0.3	0.5	6	0.8	0.25	2.3	0.1	-1.5	-1.4	26
2	0.6	0.9	2	1.5	0.25	2.8	0.2	-1.3	-1.3	35
3	0.2	0.3	50	0.5	0.25	2.0	0.1	-1.5	-1.3	46
4	0.1	0.2	18	0.3	0.25	0.0	0.0	0.3	0.5	62
Mean	0.3	0.5	19	0.8	0.25	1.8	0.1	-1.0	-0.9	42

† The overall net herbivore effect was estimated as the sum of N deposition by herbivores and rainfall, minus N consumed and N lost via ammonia volatilization.

to adaptations of grasses such as *Cynodon* spp. to short growing seasons, consistent with previous findings that near-maximum yields from long rains are achieved within 50 days, even when abundant soil moisture lasts 80–200 days (Cassady 1973). Low RUE in 2001 could also be related to a community-level effect of grass tuft mortality during the drought, particularly on nutrient-poor sites (Frank and McNaughton 1992).

Because the nutrient-enriched sites that we studied were created by fertilization with cattle manure (Augustine 2003a), many nutrients important for plant growth (N, P, Ca, K, Mg, B, Cu, Co, and Fe) increased from bushland to glade to boma study sites (Table 2). In terrestrial ecosystems, nitrogen is generally recognized as the primary nutrient limiting plant growth (Vitousek and Howarth 1991), but some grassland studies have also identified phosphorus limitations (Penning de Vries et al. 1980, Donaldson et al. 1984, Snyman 2002). Our fertilization experiment identified N as the primary limiting nutrient, but P co-limited productivity with increased N availability. Studies of grasslands in the Sahel suggest that grass N:P ratios <7 indicate strong N limitation, whereas ratios >25 indicate strong P limitation (Penning de Vries et al. 1980). In the Serengeti grasslands of Tanzania, grass leaf N:P ratios varied from only 4.6 to 5.8 across the region (McNaughton 1990), and fertilization studies showed strong N limitation throughout the ecosystem (S. J. McNaughton, unpublished data). Consistent with these findings, N fertilization at MRC increased plant N:P ratios from 5.2 to 8.0 on a site with a low soil N:P ratio. Leaf N:P ratios of 12–16 on bushland sites (Fig. 4) suggest that P co-limits grass production on bushland soils. By comparison, studies of *C. dactylon* in the United States showed that biomass N:P ratios can be extremely low, ranging only from 3.7 to 5.8 across a wide range of manure application rates (Sanderson and Jones 1997; M. A. Sanderson, personal commu-

nication). However, ratios at MRC do not reach the level indicative of sole P limitation (Penning de Vries et al. 1980). *Cynodon* leaves growing on low-P bushland soils had P concentrations (0.25–0.27%) greater than those in East African grasses grown in the lab under P-limiting conditions (0.12–0.24%; Chapin and McNaughton 1989), again suggesting that N and P co-limit grass productivity on bushland soils.

Low absolute P concentrations in bushland grasses (<0.30%) also indicate that P may affect secondary productivity because forage P concentrations of 0.40–0.60% are recommended for pregnant and lactating ruminants (McDowell 1985, Robbins 1993). The P-rich forage on glades and abandoned bomas (0.47–0.80% P) is likely to play an important role in meeting native ungulate nutritional requirements during pregnancy and lactation (McNaughton 1988, Ben-Shahar and Coe 1992).

Previous work in ecosystems dominated by migratory ungulates (Serengeti, Tanzania, and Yellowstone, USA) showed that consumption rates increased linearly with grass-layer production because the ungulates tracked landscape-level variation in productivity (Frank et al. 1998). A similar linear pattern was observed at MRC, but grazing intensity (consumption/production) was consistently greater at MRC across the entire range of ANPP (Fig. 5). The similarity in slopes among these ecosystems is striking, because in the Serengeti and Yellowstone, production and ungulate consumption vary primarily in relation to the amount of rainfall, timing of snow melt, and topographic variation in soil moisture (McNaughton 1985, Frank and McNaughton 1992). For sites with high ANPP, greater grazing intensity at MRC may be a consequence of the fact that glade and boma swards represent only a small fraction (~1%) of the total landscape. Herbivores can therefore concentrate on and maintain glades and bomas in an immature growth stage during wet seasons,

thereby encouraging continual grazing and high rates of consumption. This factor may be particularly important in high-rainfall years, consistent with significantly greater grazing intensity on glades than bushland swards during the long, postdrought growing season in 2001. For sites with low ANPP, high grazing intensity in 1999 may have been a consequence of the large annual fluctuations in rainfall that characterize this semiarid ecosystem: above-average el Niño rains in 1998 allowed cattle and impala populations to reach densities that could impose high grazing pressure throughout the landscape during the below-average rainfall conditions in 1999 (Illius and O'Connor 2000). High grazing pressure at low levels of ANPP may also be a consequence of livestock husbandry (herding and veterinary care), which leads to greater herbivore biomass per unit of primary production in managed vs. unmanaged savannas (Oesterheld et al. 1992).

Although results from several ecosystems show a linear relationship between ANPP and large herbivore consumption rates (Fig. 5; Frank et al. 1998), we also acknowledge that nonlinear relationships can occur in grazed systems. Analyses of ruminant energetic constraints predict that they will typically select swards of intermediate biomass (Wilmhurst et al. 1999, 2000), such that low consumption rates could occur on productive swards if they also attain high standing biomass. In particular, productive swards may experience low consumption rates if they grow so rapidly that grazers cannot maintain grasses in an immature growth stage, and they are subsequently avoided either due to a trade-off between forage quality and intake rate (Wilmhurst et al. 2000) or a direct reduction in foraging efficiency (Van der Koppel et al. 1996). Maximal consumption rates at intermediate levels of productivity may be most likely in systems where productive swards are spatially extensive, production is strongly pulsed in time, and the dominant herbivores do not track landscape-scale spatiotemporal variation in productivity.

Finally, our findings show that large mammalian grazers not only respond to landscape variation in soil nutrients and forage productivity, but also can affect the long-term distribution of soil and grass nutrients. During the first 40 years after a cattle boma is abandoned, N and P levels decline substantially, with N declining more rapidly than P (Augustine 2003a). Pathways of N loss during the first four decades after abandonment may include higher rates of N volatilization and leaching relative to glades, and heavy grazing pressure by cattle, which return nutrients to active bomas. However, soil N concentrations in 30–40 year old bomas are similar to concentrations in long-term glades (Augustine 2003a). As bomas age and develop into glades (>40 years old), they are used more intensively by impala, and large herbivores themselves begin to represent a net input of nitrogen (Table 3). The net input is a consequence of glade use by impala during the dry season, when minimal forage is available. Anal-

yses of impala habitat selection with automated camera monitors showed that during dry seasons, large impala herds bedded and defecated nightly in glades, most likely due to low predation risk in this shrub-free habitat, but fed daily in the surrounding bushland where green leaves, primarily of shrubs, were still available (Augustine 2002). During wet seasons, impala shifted to both bedding and foraging in glades, with significant additional grass consumption in glades by cattle. The seasonal pattern of glade selection by impala suggests that intensive use of glades is driven primarily by low predation risk in dry seasons and a combination of forage quality and low predation risk in wet seasons (Augustine 2002). Because cattle in this ecosystem graze for only 12 hours per day and excrete nutrients for 24 hours per day, their net effect on grazed swards is to remove N and redistribute it to active bomas. Although all four glades were grazed by cattle during the wet season and N consumption was similar to herbivore N deposition in glades during wet months, it was the additional dry-season N deposition by impala that resulted in a net N input from herbivores. After correcting for differential rates of N deposition in rainfall vs. loss through volatilization, the net overall herbivore effect was positive at three of the four glades, averaging 1.6 g N/m<sup>2</sup>. Although our N budget calculations are clearly subject to errors in consumption, deposition, and volatilization estimates, the fact that herbivore deposition exceeded consumption at all four replicate glades suggests that herbivore-mediated spatial redistribution of soil N is an important factor maintaining long-term glade stability. We also note that our N budget study encompassed three wet and five dry months, with the dry-season N deposition driving the positive herbivore effect. Over longer time scales, herbivores may represent a net N input during dry years (when the effects of impala dominate), but a net N loss from glades during wet years (when the effects of cattle dominate).

Our results provide empirical evidence that ungulates can maintain nutrient-rich "hot spots" in savannas, as originally hypothesized by Blackmore et al. (1990) and Young et al. (1995), but the mechanism involves more than simply ungulate attraction to nutrient-rich lawns. At MRC, the presence of native predators (spotted hyaena, leopard, wild dogs, and lion) may be an important indirect factor maintaining high dung and urine deposition in glades through their effect on impala behavior. Our findings are consistent with evidence that native ungulates often indirectly affect N cycling (Hobbs 1996), and suggest an indirect link between impala and cattle in this ecosystem: N transferred from bushland to glades by impala during dry seasons supports the rapid growth of high-quality forage in glades, which in turn is grazed intensively by both cattle and impala. Because impala increase consumption of shrub leaves during dry seasons (Hansen et al. 1985, Klein and Fairall 1986, Meissner et al.

1996), and at least one of the dominant *Acacia* species in this ecosystem symbiotically fixes  $N_2$  (Assefa and Kleiner 1998), impala may create an indirect pathway from atmospheric N to cattle. In contrast to the often antagonistic relationship between pastoralists and wildlife on Kenya's northern rangeland (de Leeuw et al. 2001), the high densities of native ungulates found on commercial rangeland in central Kenya may provide some indirect benefits to livestock through the maintenance of highly productive, nutrient-rich patches within the landscape, in addition to their contribution to the district's economy through tourism and game meat.

At bushland sites, large herbivores represented a net loss of N (Table 3) as well as a permanent loss of P (Augustine 2003a). Grazing on these sites was primarily by cattle, which return large quantities of dung and urine to overnight bomas. Bomas are eventually abandoned and contribute further to the patchy distribution of soil and grass nutrients in the ecosystem. Grazing pressure in the bushland landscape is heterogeneously distributed (Table 3), and the degree to which the documented N loss from our bushland sites applies to the overall landscape is unclear. Although cattle management via bomas enhances the availability of nutrient-rich forage across the landscape through glade creation, this nitrogen is withdrawn from the bushland landscape, with localized losses as high as 1.5 g N/m<sup>2</sup> over an 8-month period (Table 3). The degree to which locally intense grazing on some bushland sites combined with N and P loss to bomas could contribute to rangeland degradation, especially through increased soil erosion and irreversible declines in productivity (Rietkirk et al. 1997), has not been addressed. Theoretical analyses of soil–grass–grazer interactions predict that the net N loss at bushland sites will be associated with a negative grazer effect on productivity, whereas the net positive effect of herbivores on glade N balance will promote productivity (de Mazancourt et al. 1998).

Recent debate over the productivity and stability of African rangelands has focused on the application of equilibrium vs. non-equilibrium frameworks to management and development policies in arid and semiarid regions, and has primarily emphasized the importance of annual variation in rainfall (Ellis and Swift 1988, Behnke and Scoones 1993, Illius and O'Connor 1999, 2000). At MRC, the long-term coefficient of variation in annual rainfall (44%) exceeds the 30% level suggested by Ellis et al. (1993) as being typical of non-equilibrium rangelands better characterized by variation in rainfall than by the mean. Variation in cattle densities at MRC during our study also followed the model of Ellis et al. (1993) in which herders and managers responded to a single-year drought by moving cattle to distant ranches that received greater rainfall, and then rapidly re-stocking MRC when rains resumed. However, at more local scales (within the seasonal range of

a cattle or impala herd) and within years (during any given wet season), soil N and P limit grass-layer productivity in this climatically variable and intensively grazed semiarid ecosystem. Because ranch managers rarely consider the ecosystem-level implications of nutrient redistribution, boma placement and relocation rates are primarily managed in relation to the short-term needs of livestock. However, these management decisions determine the long-term distribution of nutrient "hot spots" within the landscape, which in turn affects the spatial distribution of herbaceous production, forage nutrient content, and large herbivore consumption rates. In terms of meeting the nutritional requirements of large herbivores, nutrient-rich grazing lawns probably are a key wet-season resource, particularly for pregnant and lactating animals. Although cattle management via bomas determines the distribution of these lawns, native impala play an important role in their maintenance by concentrating N into glades during dry seasons.

#### ACKNOWLEDGMENTS

We especially thank F. Lomojo, J. Ekiru, and D. M. Augustine for their assistance and enthusiasm with all aspects of field data collection, and M. McNaughton for her assistance with soil nutrient analyses. R. W. Ruess, N. T. Hobbs, and an anonymous reviewer provided many helpful comments on the manuscript. We thank the Office of the President of the Republic of Kenya for permission to conduct this research in Kenya. Financial support was provided by the National Geographic Society, an NSF pre-doctoral fellowship to D. J. Augustine, and NSF grants DEB-9813050 and DEB-9903845 to S. J. McNaughton.

#### LITERATURE CITED

- Ahn, P. M., and L. C. Geiger. 1987. Kenya soil survey—soils of Laikipia District. Ministry of Agriculture, National Agricultural Laboratories, Kabete, Kenya.
- Andere, D. K. 1981. Wildebeest *Connochaetes taurinus* (Burchell) and its food supply in Amboseli Basin. *African Journal of Ecology* **19**:239–250.
- Assefa, S., and D. Kleiner. 1998. Nodulation pattern and acetylene reduction (nitrogen fixation) activity of some highland and lowland *Acacia* species of Ethiopia. *Biology and Fertility of Soils* **27**:60–64.
- Augustine, D. J. 2002. Large herbivores and process dynamics in a managed savanna ecosystem. Dissertation, Syracuse University, Syracuse, New York, USA.
- Augustine, D. J. 2003a. Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. *Journal of Applied Ecology* **40**:137–149.
- Augustine, D. J. 2003b. Spatial heterogeneity in the herbaceous layer of an East African savanna. *Plant Ecology*, in press.
- Augustine, D. J., and D. A. Frank. 2001. Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. *Ecology* **82**:3149–3162.
- Behnke, R., and I. Scoones. 1993. Rethinking range ecology: implications for rangeland management in Africa. Pages 1–30 in R. Behnke, I. Scoones, and C. Kerven, editors. *Range ecology at disequilibrium*. Overseas Development Institute, London, UK.
- Bell, R. V. H. 1982. The effect of soil nutrient availability on community structure in African ecosystems. Pages 193–216 in B. J. Huntley and B. H. Walker, editors. *Ecology of*

- tropical savannas. Springer-Verlag, New York, New York, USA.
- Ben-Shahar, R., and M. Coe. 1992. The relationships between soil factors, grass nutrients and the foraging behaviour of wildebeest and zebra. *Oecologia* **90**:422–428.
- Blackmore, A. C., M. T. Mentis, and R. J. Scholes. 1990. The origin and extent of nutrient-enriched patches within a nutrient-poor savanna in South Africa. *Journal of Biogeography* **17**:463–470.
- Carl, G., and R. Brown. 1985. Protein requirement of collared peccaries. *Journal of Wildlife Management* **49**:351–355.
- Cassady, J. 1973. The effect of rainfall, soil moisture and harvesting intensity on grass production on two rangeland sites in Kenya. *East African Agricultural and Forestry Journal* **39**:26–36.
- Chapin, F., and S. J. McNaughton. 1989. Lack of compensatory growth under phosphorous deficiency in grazing-adapted grasses from the Serengeti Plains. *Oecologia* **79**:551–557.
- de Leeuw, J., M. Waweru, O. Okello, M. Maloba, P. Nguru, M. Said, H. Aligula, I. Heitkonig, and R. Reid. 2001. Distribution and diversity of wildlife in northern Kenya in relation to livestock and permanent water points. *Biological Conservation* **100**:297–306.
- de Mazancourt, C., M. Lorea, and L. Abbadie. 1998. Grazing optimization and nutrient cycling: when do herbivores enhance plant production? *Ecology* **79**:2242–2252.
- Detling, J. 1988. Grasslands and savannas: regulation of energy flow and nutrient cycling by herbivores. Pages 131–148 in L. Pomeroy and J. Alberts, editors. *Concepts of ecosystem ecology: a comparative view*. Springer-Verlag, New York, New York, USA.
- Donaldson, C., G. Rootman, and D. Grossman. 1984. Long term nitrogen and phosphorous application to veld. *Journal of the Grassland Society of South Africa* **1**:27–32.
- Ellis, J. E., M. B. Coughenour, and D. M. Swift. 1993. Climate variability, ecosystem stability, and the implications for range and livestock development. Pages 31–41 in R. Behnke, I. Scoones, and C. Kerven, editors. *Range ecology at disequilibrium*. Overseas Development Institute, London, UK.
- Ellis, J. E., and D. M. Swift. 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. *Journal of Range Management* **41**:450–459.
- Frank, D. A., R. Inouye, N. Huntly, G. Minshall, and J. Anderson. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. *Biogeochemistry* **26**:163–188.
- Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. *Ecology* **73**:2043–2058.
- Frank, D. A., S. J. McNaughton, and B. F. Tracy. 1998. The ecology of the earth's grazing ecosystems: comparing the Serengeti and Yellowstone. *BioScience* **48**:513–521.
- Georgiadis, N., and S. J. McNaughton. 1988. Interactions between grazers and a cyanogenic grass, *Cynodon plectostachyus*. *Oikos* **51**:343–350.
- Hansen, R., M. Mubambi, and S. Bauni. 1985. Diets and trophic ranking of ungulates of the northern Serengeti. *Journal of Wildlife Management* **43**:823–827.
- Hintz, H., and H. Schryver. 1972. Nitrogen utilization in ponies. *Journal of Animal Science* **34**:592–594.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* **60**:695–713.
- Holter, J., H. Hayes, and S. Smith. 1979. Protein requirement of yearling white-tailed deer. *Journal of Wildlife Management* **43**:872–879.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* **22**:477–503.
- Illius, A., and T. O'Connor. 1999. On the relevance of non-equilibrium concepts to arid and semiarid grazing systems. *Ecological Applications* **9**:798–813.
- Illius, A., and T. O'Connor. 2000. Resource heterogeneity and ungulate population dynamics. *Oikos* **89**:283–294.
- Izraely, H., I. Choshniak, C. Stevens, and A. Shkolnik. 1989. Energy digestion and nitrogen economy of the domesticated donkey (*Equus asinus asinus*) in relation to food quality. *Journal of Arid Environments* **17**:97–101.
- Keya, N. 1973. The effect of N. P. fertilizers on the productivity of *Hypharrena* grassland. *East African Agricultural and Forestry Journal* **39**:195–200.
- Klein, D., and N. Fairall. 1986. Comparative foraging behaviour and associated energetics of impala and blesbok. *Journal of Applied Ecology* **23**:489–502.
- McDowell, L. R. 1985. Detection of mineral status of grazing ruminants. Pages 339–357 in L. R. McDowell, editor. *Nutrition of grazing ruminants in warm climates*. Academic Press, Orlando, Florida, USA.
- McNaughton, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* **55**:259–294.
- McNaughton, S. J. 1988. Mineral nutrition and spatial concentrations of African ungulates. *Nature* **334**:343–345.
- McNaughton, S. J. 1990. Mineral nutrition and seasonal movements of African migratory ungulates. *Nature* **345**:613–615.
- McNaughton, S. J., D. G. Milchunas, and D. A. Frank. 1996. How can net primary productivity be measured in grazing ecosystems? *Ecology* **77**:974–977.
- McNaughton, S. J., R. W. Ruess, and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. *BioScience* **38**:794–800.
- Meissner, H. H., E. Pieterse, and J. H. J. Potgieter. 1996. Seasonal food selection and intake by male impala *Aepyceros melampus* in two habitats. *South African Journal of Wildlife Research* **26**:56–63.
- Mould, E., and C. Robbins. 1981. Nitrogen metabolism in elk. *Journal of Wildlife Management* **45**:323–334.
- Oba, G., N. C. Stenseth, and W. J. Lusigi. 2000. New perspectives on sustainable grazing management in arid zones of sub-saharan Africa. *BioScience* **50**:35–51.
- O'Connor, T. G. 1985. A synthesis of field experiments concerning the grass layer in the savanna regions of southern Africa. *South African National Scientific Programme Report Number 114*, Pretoria, South Africa.
- Oesterheld, M., O. Sala, and S. McNaughton. 1992. Effect of animal husbandry on herbivore-carrying capacity at a regional scale. *Nature* **356**:234–236.
- Pandey, C. B., and J. S. Singh. 1992. Rainfall and grazing effects on net primary productivity in a tropical savanna, India. *Ecology* **73**:2007–2021.
- Pastor, J., B. Dewey, R. Moen, D. J. Mladenoff, M. White, and Y. Cohen. 1998. Spatial patterns in the moose-forest-soil ecosystem on Isle Royale, Michigan, USA. *Ecological Applications* **8**:411–424.
- Penning de Vries, F. J. Krul, and H. van Keulen. 1980. Productivity of Sahelian rangelands in relation to the availability of nitrogen and phosphorous from the soil. Pages 95–113 in T. Rosswall, editor. *Nitrogen cycling in West African ecosystems*. Royal Swedish Academy of Science, Stockholm, Sweden.
- Plumptre, A. J., and S. Harris. 1995. Estimating the biomass of large mammalian herbivores in a tropical montane forest: a method of faecal counting that avoids a 'steady state' system. *Journal of Applied Ecology* **32**:111–120.
- Reid, R. S., and J. E. Ellis. 1995. Impacts of pastoralists on woodlands in south Turkana, Kenya: livestock-mediated tree recruitment. *Ecological Applications* **5**:978–992.
- Reitnour, C., and J. Treece. 1970. Relationship of nitrogen source to certain blood components and nitrogen balance in the equine. *Journal of Animal Science* **32**:487–490.



- Rietkerk, M., F. Van den Bosch, and J. Van de Koppel. 1997. Site-specific properties and irreversible vegetation changes in semi-arid grazing system. *Oikos* **80**:241–252.
- Robbins, C. T. 1993. *Wildlife feeding and nutrition*. Academic Press, San Diego, California, USA.
- Ruess, R., and S. McNaughton. 1988. Ammonia volatilization and the effects of large grazing mammals on nutrient loss from East African grasslands. *Oecologia* **77**:382–386.
- Ruess, R., and S. Seagle. 1994. Landscape patterns in soil microbial processes in the Serengeti National Park, Tanzania. *Ecology* **75**:892–904.
- Sanderson, M., and R. Jones. 1997. Forage yields, nutrient uptake, soil chemical changes, and nitrogen volatilization from bermudagrass treated with dairy manure. *Journal of Production Agriculture* **10**:266–271.
- Scholefield, D., D. R. Lockyer, D. C. Whitehead, and K. C. Tyson. 1991. A model to predict transformations and losses of nitrogen in UK pastures grazed by beef cattle. *Plant and Soil* **132**:165–177.
- Seagle, S. W., and S. J. McNaughton. 1992. Spatial variation in forage nutrient concentrations and the distribution of Serengeti grazing ungulates. *Landscape Ecology* **7**:229–241.
- Slade, L., D. Robinson, and K. Casey. 1970. Nitrogen metabolism in nonruminant herbivores I. The influence of non-protein nitrogen and protein quality on the nitrogen retention of adult mares. *Journal of Animal Science* **30**:753–760.
- Snyman, H. 2002. Short-term response of rangeland botanical composition and productivity to fertilization (N and P) in a semi-arid climate of South Africa. *Journal of Arid Environments* **50**:167–183.
- Stelfox, J. B. 1986. Effects of livestock enclosures (bomas) on the vegetation of the Athi Plains, Kenya. *African Journal of Ecology* **24**:41–45.
- Turner, M. D. 1998. Long-term effects of daily grazing orbits on nutrient availability in Sahelian West Africa: 1. Gradients in the chemical composition of rangeland soils and vegetation. *Journal of Biogeography* **25**:669–682.
- Van de Koppel, J., J. Huisman, R. Van der Wal, and H. Olff. 1996. Patterns of herbivory along a productivity gradient: an empirical and theoretical investigation. *Ecology* **77**:736–745.
- Vitousek, P. M., and R. W. Howarth. 1991. Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* **13**:87–115.
- Weisberg, S. 1985. *Applied linear regression*. Second edition. John Wiley, New York, New York, USA.
- Wilmshurst, J., J. Fryxell, and C. Bergman. 2000. The allometry of patch selection in ruminants. *Proceedings of the Royal Society of London Series B* **267**:345–349.
- Wilmshurst, J., J. Fryxell, B. Farm, A. Sinclair, and C. Henschel. 1999. Spatial distribution of Serengeti wildebeest in relation to resources. *Canadian Journal of Zoology* **77**:1223–1232.
- Young, T. P., N. Partridge, and A. Macrae. 1995. Long-term glades in acacia bushland and their edge effects in Laikipia, Kenya. *Ecological Applications* **5**:97–108.