Journal of Applied Ecology 2003
40, 137–149

Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna

DAVID J. AUGUSTINE
Department of Biology, Syracuse University, Syracuse, NY 13244, USA

Summary

1. The effect of livestock on African rangelands has been a major focus of recent research, but little attention has been paid to the way livestock affects the distribution and availability of soil nutrients. In East African savannas, overnight containment of livestock in thorn-scrub corrals or 'bomas' concentrates large quantities of nutrients into small areas, potentially altering the landscape distribution of nitrogen (N) and phosphorus (P) in soils and plants.

2. This study was designed to (i) measure the density, turnover rates and soil nutrient concentrations of abandoned cattle bomas on nutrient-poor rangeland in central Kenya; (ii) determine whether long-term glades dominated by *Cynodon plectostachyus* are derived from abandoned bomas; and (iii) evaluate the effect of cattle bomas on the landscape-level distribution of N and P.

3. In the study area, glades (> 39 years old) averaged 0·71 ha in size and occurred at a density of 0·71 km^{-2}. Abandoned bomas (1–39 years since abandonment) averaged 0·39 ha and occurred at a density of 1·21 km^{-2}. During 1961–2000, no glades reverted to bushland vegetation, while 53 bomas were abandoned.

4. All characteristics of soils measured across a boma–glade chronosequence indicated glades were indeed derived from abandoned bomas. Soil N, P and organic matter quality in the surface (0–15 cm) layer were similar for glades and 30–39-year-old bomas, but were significantly enriched relative to surrounding bushland. In contrast, at 40–65 cm depth beneath bomas, glades and bushland, soil N was similar. The texture of surface soils from bomas, glades and bushland was similar, indicating glades were not derived from a unique parent material.

5. Leaves of *C. plectostachyus* from 12–24-year bomas and long-term glades were enriched in P, calcium (Ca) and N relative to leaves of *Cynodon dactylon* from nearby bushland sites. In particular, P in boma and glade grass was above recommended levels for growing and lactating livestock, while P content of bushland grass was lower than recommended levels.

6. Cattle management via bomas exerts a greater effect on the distribution of P relative to N within the landscape. For cattle grazing an area of 20–25 km^2 $boma^{-1}$, an estimated 0·24–0·30 g N m^{-2} $year^{-1}$ is removed from the rangeland and deposited into bomas. Within 1·5 years of boma abandonment, 70% of this N is already lost from the manure and upper soil layer. Permanent N loss does occur via leaching, but the majority is probably volatilized and redistributed in rainfall. N deposition in rainfall (0·43 g N m^{-2} $year^{-1}$) is more than sufficient to offset losses due to cattle grazing and deposition in bomas. In contrast, P deposited in bomas is more tightly retained, creating small P-enriched 'hotspots' while causing a permanent loss of the order of 0·021–0·026 g P m^{-2} $year^{-1}$ from the surrounding bushland landscape.

7. *Synthesis and applications.* Results indicate that abandoned bomas persist as nutrient-enriched patches for at least four decades. Rangeland managers should recognize that the placement and relocation rate of current bomas influences the long-term distribution and availability of nutritionally important forage for livestock and wildlife. Future assessments of African rangeland stability should incorporate not only direct effects of

Correspondence: David J. Augustine, 200 Biological Research Laboratories, Syracuse University, Syracuse, NY 13244, USA (fax +315 443 2012; e-mail djaugust@syr.edu).

livestock and rainfall on vegetation, but also the spatial effects of livestock management on soil and plant nutrients.

Key-words: ammonia volatilization, cattle bomas, Kenya, nutrient hotspots, pastoral settlements, rangeland nutrient dynamics, ungulates, wildlife habitat.

Journal of Applied Ecology (2003) **40**, 137–149

Introduction

Abandoned cattle corrals or 'bomas' are a widespread feature of semi-arid rangelands in East Africa. Bomas are temporary structures consisting of a dense ring of thorn-scrub branches that contain and protect livestock overnight from theft and predation. An additional consequence of boma use is the concentration of large quantities of dung and urine within a small area, containing plant nutrients harvested from the surrounding savanna. Following abandonment, bomas often support a unique plant community and potentially alter the spatial pattern of nutrient cycling within the ecosystem. For example, in Turkana district of northern Kenya, old bomas contained six to nine times more soil nitrogen (N) and phosphorous (P) than surrounding habitats and supported thickets of regenerating *Acacia tortilis* (Reid & Ellis 1995). In southern Kenya, abandoned bomas were dominated by a lawn of *Cynodon nlemfuensis*, with enriched concentrations of nutrients both in soils and grasses (Stelfox 1986).

In Laikipia district of central Kenya, Young, Partridge & Macrae (1995) described a two-phase mosaic within the savanna landscape consisting of small grassland glades, dominated by a short-statured sward of *Cynodon plectostachyus*, dispersed within an *Acacia*-dominated bushland community containing a more diverse perennial grass understorey. Based on the distinct community composition, enriched soil nutrient characteristics and consistent topographic position of *Cynodon*-dominated glades, Young, Partridge & Macrae (1995) hypothesized that glades originated from abandoned Maasai settlements that had persisted for decades. Studies in South Africa also suggest that particular plant communities are derived from abandoned sites of human occupation that have persisted in a nutrient-enriched state for centuries (Blackmore, Mentis & Scholes 1990). In both these cases, nutrient-enriched communities are intensively grazed and browsed by native ungulates and cattle, and potentially enhance the long-term density of large herbivores the ecosystem can support (Blackmore, Mentis & Scholes 1990; Young, Partridge & Macrae 1995).

On nutrient-poor rangelands, the redistribution of soil nutrients via cattle bomas could have significant consequences, not only for the nutrient-enriched plant community that develops after abandonment but also for the surrounding landscape from which nutrients are withdrawn. Although the effect of cattle on African rangelands has been a major focus of recent research (Behnke, Scoones & Kerven 1993; Weber *et al.* 1998; Illius & O'Connor 1999; Fynn & O'Connor 2000), few studies have considered the indirect effects cattle may exert on rangelands through the redistribution of soil nutrients. In particular, soil N and P can both limit grass productivity in many semi-arid African rangelands (Keya 1973; O'Connor 1985; Turner 1998b) and can influence local and regional distributions of ungulate herbivores (McNaughton 1988; Ben-Shahar & Coe 1992; Seagle & McNaughton 1992). However, little is currently known regarding the magnitude of nutrient inputs to bomas, their pattern and pathways of nutrient loss over time, or whether abandoned bomas indeed are the precursors of persistent nutrient-enriched communities within the landscape.

This study concerned a chronosequence of cattle bomas, ranging in age from 1 to 39 years since abandonment, and long-term glades (> 39 years old) within the same region in central Kenya studied by Young, Partridge & Macrae (1995). The study region was underlain by sandy nutrient-poor soils developed from basement, metamorphic parent material (Ahn & Geiger 1987) and hence represents a landscape where the redistribution of limited nutrient pools by cattle could have an ecologically important effect on forage nutrients and hence on cattle and other large herbivores themselves. Objectives of this study were to (i) measure the size and density of glades and bomas; (ii) evaluate rates of boma appearance and glade disappearance over the period 1961–2000; (iii) determine whether long-term glades are derived from abandoned bomas; and (iv) evaluate the potential effects of bomas on the redistribution of N and P within the landscape. To examine whether glades are derived from bomas (objective iii), five specific predictions were tested concerning soil nutrient concentrations: (i) the massive input of manure to bomas creates a highly N-enriched upper soil layer, which declines in nutrient concentrations following abandonment, while nutrient concentrations in deep soil layers are similar across boma, glade and bushland sites; (ii) organic matter quality in glades is similar to old bomas but distinctly different from the surrounding bushland soils; (iii) P concentrations in the surface soils of glades are similar to levels in old bomas but highly enriched relative to bushland soils; (iv) the texture of glades and boma soil is similar to soils from the surrounding bushland; and (v) if the study sites represent a chronosequence, then rates of soil mineral loss during organic matter decomposition should follow the sequence Na > K > Mg > Ca

(Schlesinger 1997). To evaluate the effects of bomas on N and P redistribution within the landscape (objective iv), amounts of N and P deposited into a boma were estimated together with corresponding removal rates from the surrounding landscape. Estimates of boma N inputs were compared to amounts measured 1·5 years after abandonment to evaluate the potential for N loss from bomas via leaching and volatilization. Finally, the amount of N removed from grazed rangeland on an areal basis was compared with the rate of N deposition in rainfall.

Study area

All research was conducted at the Mpala Research Centre and associated Mpala ranch (MRC), which encompasses 190 km^2 of semi-arid savanna within the Laikipia district of central Kenya (37°53′E, 0°17′N). The landscape surveyed in this study is underlain by soils classified as well drained, moderate to very deep, friable sandy loams developed from metamorphic basement rocks (Ahn & Geiger 1987). Mean annual rainfall is 500 mm (coefficient of variation = 0·35), with wet seasons typical during April–May, August and October, and a consistent dry season during January–March. Abandoned bomas and long-term glades are distributed within a background *Acacia*-dominated bushland community. Glades and older bomas are dominated by a short-statured sward of *Cynodon plectostachyus* and lack shrubs. In younger bomas, the annual forb *Gynandropsis gynandra* is abundant during certain rain cycles. In older bomas and glades, the annual forb *Tribulus terrestris*, the sedges *Cyperus blysmoides* and *Cyperus cristatus* and the grass *Sporobolus pellucidus* often occur within the *Cynodon*-dominated lawn (D. J. Augustine, personal observation). The surrounding bushland contains a heterogeneous mosaic of bare soil and perennial grass dominated by *Digitaria milanjiana*, *Cynodon dactylon*, *Pennisetum mezianum* and *Pennisetum stramineum*, and woody vegetation is dominated by *Acacia brevispica*, *Acacia mellifera* and *Acacia etbaica* (Young, Partridge & Macrae 1995).

Since at least 1800, the Laikipiak Maasai have occupied and maintained livestock in the region. Their numbers were reduced by a combination of factors including rinderpest and warfare in the early 1900s, and the majority of Maasai left Laikipia following a treaty with the British in 1911 (Young, Partridge & Macrae 1995). Since that time, most of Laikipia, including MRC, has been privately owned rangeland.

At MRC, livestock have been managed for market production using traditional pastoral herding methods, with both Maasai and Turkana herders hired to maintain the cattle over the past several decades. Between 1990 and 2000, around 1400–3100 cattle have been maintained at MRC, with peak numbers occurring after high-rainfall years in 1997 and 1998, and minimum numbers after a severe drought in 2000. In the past, sheep and goats were also kept on MRC, but cattle are currently the primary livestock species. Cattle are contained overnight in bomas constructed from *A. mellifera* and *A. etbaica*. The ranch manager is ultimately responsible for deciding the number, location and rotation pattern of bomas. A single boma typically consists of several adjacent paddocks containing three herds of 120 cattle each, and six to eight active bomas are usually maintained on MRC. The most common native grazers and mixed-feeders are impala *Aepyceros melampus*, zebra *Equus burchellii*, waterbuck *Kobus ellipsiprymnus*, buffalo *Syncerus caffer* and eland *Taurotragus oryx*. Native predators include spotted hyaena *Crocuta crocuta*, lion *Panthera leo* and leopard *Panthera pardus*. Plant nomenclature follows Polhill (1972, 1974, 1982) for grasses and Blundell (1987) for forbs and shrubs. Mammal nomenclature follows Kingdon (1997).

Methods

FIELD METHODS

The number and size of bomas and long-term glades were measured within three study areas located in the north, central and southern regions of MRC. The northern region was 16 km^2, the central region 14 km^2, and the south 12 km^2. Within each area, all known bomas and glades were identified based on interviews with herders and extensive ground searches conducted in 1999 and 2000. Glades and bomas were identified by their distinctive short-statured sward dominated by *C. plectostachyus* and the lack of shrub seedlings or saplings. GPS (Global Positioning System) locations of each site were recorded, and size was measured using the distribution of *C. plectostachyus* to define glade and boma edges. The presence and extent of any other perennial grass species within each site, as well as any shrubs growing along old fence lines, were also noted.

Aerial photographs taken in 1961 and 1969 were used to differentiate glades from bomas and to measure rates of boma and glade appearance and disappearance. Glades were defined as sites appearing as open grassland patches in the 1961 aerial photo with no visible fence lines. Sites with visible fence lines were designated as bomas. Both glades and bomas exhibited a distinctive reflectance in the aerial photos, probably due to the continuous grass cover in glades and the continuous dung layer in active or recently abandoned bomas. The number of long-term glades in each study area in 1961, the number of active bomas in 1961, and the number of new bomas appearing between 1961 and 1969 were determined from aerial photos. Glades and bomas located during the ground survey in 2000 were plotted on a study area map and compared with the aerial photos to determine glade appearance and disappearance rates during 1961–2000.

Soils were collected from a chronosequence consisting of two recently abandoned bomas (each 1·5 years old), five bomas abandoned 12–24 years ago, five bomas abandoned 30–39 years ago, and eight long-term glades present in the 1961 aerial photo. The year of abandonment for each of the 12–24-year-old bomas was determined from interviews with at least two herders and/or ranch managers. The 30–39-year-old bomas were aged based on their presence in the 1961 and/or 1969 aerial photos.

At each site, four randomly located soil cores were collected in July 1999 and divided into 0–15, 15–40 and 40–65-cm depths. Cores from 15–65-cm depths were collected at all bomas but only four glades. For sites where only total soil nutrient pools were measured, soils were air-dried and returned to Syracuse University (SU; Syracuse, USA). For a subset of sites (see below), inorganic N pools were also measured. Cores from these sites were placed in a whirl-pak bag (Fisher Scientific, Pittsburgh, PA, USA), immediately stored on ice in a cooler, returned to the MRC laboratory, and maintained at 4 °C until extraction with 1 M KCl within 48 h of collection. For the two recently abandoned bomas, we differentiated between a dung layer and mineral soil. Six cores were collected from the dung layer plus mineral soil at each of the three depths, and dung layer depth was measured every 5 m along transects bisecting two paddocks.

Soil cores (0–15 cm depth) were also collected from the surrounding bushland landscape at 46 points distributed systematically across the three study areas with 1-km spacing between points (16 points in the north, 18 in the central region and 12 in the south). Thus, sampling points were evenly distributed across the entire 42 km^2 area in which bomas and glades were studied. All bushland sampling points were > 50 m from a glade or boma edge. At four bushland sites located *c.* 200 m from each of four long-term glades, eight soil cores were collected to a depth of 65 cm (four beneath shrubs and four between shrubs), with cores divided into 0–15, 15–40 and 40–65-cm layers.

Leaves from dominant grasses at boma, glade and bushland sites were also collected for nutrient analyses. *Cynodon plectostachyus* only occurred on glades and abandoned bomas and hence could not be sampled across all soil types. At bushland sites, *C. dactylon* was sampled because this is a dominant species on bushland soils, has a stoloniferous growth form similar to *C. plectostachyus*, and is also a preferred forage species for large ungulates. At each of four 12–24-year abandoned bomas, four long-term glades and four bushland sites located *c.* 200 m from the glades, 20 of the youngest, fully expanded *Cynodon* leaves were collected from four randomly located 1-m^2 plots. Leaves were sampled in August 1999 near the peak of a 1-month growing season.

INORGANIC N POOLS AND LEACHING

Relative leaching rates and inorganic N pools across soil depths were examined for a subset of the study sites consisting of two recently abandoned bomas, four 12–20-year bomas, three long-term glades and three bushland sites paired to each glade. Ion-exchange resin bags (Binkley 1984) were used to assess leaching rates. Nylon bags containing two level tablespoons (29·6 ml) of mixed-bed ion-exchange resin (Dowex MR-3; a 1 : 1 mixture of HCRS[H$^+$] and SBR[OH$^-$], Dow Chemical Co., Midland, Michigan, USA) were buried at a depth of 65 cm during March and retrieved in late July 1999. For each bag, a hole was excavated to a depth of 75 cm. At 65-cm depth, a space for the resin bag was excavated parallel to the ground surface and 15 cm inward from the original hole. After placement of the resin bag, soil was carefully repacked into place. Sample size at each site was the same as the number of soil cores collected. Sites received 190–250 mm rainfall during the incubation period.

SOIL AND PLANT ANALYSES

Total N and carbon (C) content of soils and grass tissue were analysed by Dumas combustion with a Carlo-Erba CN Analyser (Milan, Italy). Total P, potassium (K), calcium (Ca), magnesium (Mg) and sodium (Na) of soils and grass tissue was measured by inductively coupled plasma spectroscopy (Leman Laboratories PS3000, Hudson, MA) in simultaneous mode following procedures described by McNaughton (1988). Soil organic matter was measured by weight loss after heating soils originally dried at 105 °C to 500 °C. For a subset of sites (see above) and for the dung layer in the case of recently abandoned bomas, inorganic N (NO_3 + NH_4) was measured at each soil depth. For these cores, a 10-g subsample was extracted with 50 ml 1 M KCl, shaken immediately after extraction and again at 12 h, and then filtered at 24 h. Extracts were preserved with phenylmercuric acetate and frozen, except during shipment from MRC to SU. Extracts were analysed for NO_3^- and NH_4^+ concentrations by continuous flow analysis (Lachat Quikchem AE, Milwaukee, WI). Gravimetric moisture content was determined for a 15-g subsample of each core after oven drying at 60–80 °C. All nutrient concentrations are reported on a soil dry-weight basis. Sand content of a composite soil sample from each site was determined by sieving.

STATISTICAL ANALYSES

To examine variation in soil nutrients and organic matter quality across the abandoned boma–glade chronosequence, sites were grouped into five age classes: 1·5-year bomas (two sites), 12–24-year bomas (five), 30–39-year bomas (five), long-term glades (eight) and bushland sites (46). One-way ANOVA applied to the natural log-transformed geometric mean for each site and post-hoc pairwise comparisons (Tukey HSD) were used to examine differences among these five groups. To examine variation in organic matter quality among sites, the ratio of soil carbon to total organic matter (OM) was used. In forest soils, this ratio declines with depth. Typical values are 0·5–0·6 in the 0–10-cm layer and 0·33–0·46 below 20-cm depth (Huntington *et al.*

1989; Johnson 1995). Lower C:OM ratios indicate greater relative content of oxygen-containing functional groups (C = O, COOH and COH), which reflects an increase in the amount of fulvic acids and humin relative to humic acids during decomposition (Huntington *et al.* 1989; Rice & MacCarthy 1991).

BOMA N AND P INPUTS

The amount of N and P deposited in a boma was estimated using two independent methods. The first was a direct measure of N and P in soil cores collected from two bomas abandoned 1·5 years previously. N and P concentrations from the dung layer were converted to g m^{-2} based on measures of mean dung depth taken every 5 m along transects bisecting two paddocks at each site. Bulk densities for the dung and 0–15-cm soil layers were determined by weighing whole cores and correcting for moisture content. Deposition into the two recently abandoned bomas was calculated as the sum of N and P in the dung layer and the 0–15-cm soil layer minus the amount of N and P in the 0–15-cm layer of soil cores collected from a bushland site located at the same topographic position approximately 500 m from each boma. Deeper soil layers were not included if differences between the boma and adjacent bushland site were not significant. Total N and P in bushland soils was calculated assuming 28% of the bushland site area was beneath shrub canopies (D. J. Augustine, unpublished data).

The second method estimated N and P deposition into a boma based on the following measurements and assumptions. It was assumed that the boma was stocked with 360 cattle, the usual current practice at MRC. Boma size was estimated as the mean size of the two recently abandoned bomas, as measured during the ground survey. Cattle defecation rate was measured by following seven different cows each for a 10–12-h period during April and May 2000, and recording all defecation events. Mean dung group weight was calculated from 49 groups collected fresh during January 1999–February 2000. For each group, the wet weight was recorded and then converted to dry weight based on water content of a 15–30-g subsample oven-dried at 60–80 °C for 48 h. Dung N and P content were measured for a randomly selected subsample of 14 dry season samples and all 12 wet season samples using the same methods described previously for soils. These parameters were used to estimate N and P excretion in dung by a single cow over 12 h. The amount of N excreted in dung vs. urine reflects the concentration of N in the diet. For cattle, Scholefield *et al.* (1991) reported that 45% of N is excreted in the urine for a diet containing 1·5% N, with the amount excreted in urine increasing linearly to a maximum of 80% for a diet containing 4·0% N. Based on this relationship, urine excretion rates were set at 45% during the dry season (urine:dung N excretion ratio of 0·82) and 66% during the wet season (urine:dung N excretion ratio of 1·94, corresponding to a diet of 3% N). Urine-N excretion rate was estimated as a multiple of the dung-N excretion rate, using the different constants for wet and dry seasons.

Based on the estimates of N and P deposition into a boma, the amounts that must be removed from the surrounding rangeland were calculated. For comparison, N deposited in rainfall was measured during January–July 1999 by collecting monthly rainfall samples. Rain samples were frozen until analysis for NO_3 and NH_4 content using the same methods described for soil KCl extracts.

Results

GLADE AND BOMA ABUNDANCE

From the 1961 aerial photo, 31 long-term glades and eight active bomas were identified. Of the glades, 27 still persisted as distinct glades dominated by short-statured *C. plectostachyus* in 2000 and one was replaced by a new boma (Table 1). The three remaining glades persisted as shrub-free patches containing some areas of short-statured *Cynodon*, but *Cynodon* in these three sites was more patchily distributed and *Pennisetum mezianum* had invaded over 25% of the area. In 2000, glades averaged 0·71 ha and occurred at a density of 0·71 km^{-2} or 0·51% of the study area. During the ground survey, 53 abandoned bomas were identified. These averaged 0·40 ha in size, occurred at a density of 1·21 km^{-2} and covered 0·47% of the landscape. Two bomas observed in the 1961 photos were not identified in the ground survey. These two sites were small (< 0·15 ha), lacked a short-statured *Cynodon* lawn and contained shrub seedlings.

SOIL CHARACTERISTICS ALONG A BOMA–GLADE CHRONOSEQUENCE

Differences in soil organic matter quality (indexed by C:OM ratios) and soil N and P content among study sites were consistent with the hypothesis that glades are derived from abandoned bomas. First, C:OM ratios of the dung layer from recently abandoned

Table 1. Numbers and turnover of glades and abandoned bomas within a 42-km^2 study area

Glade abundance and turnover	
Glades present in 1961	31
Glades still present in 2000	27
Glades with *Pennisetum* invasion	3
Glades converted to a new boma	1
Abandoned boma appearance and turnover	
Bomas present in 1961	8
New bomas in 1969	3
New bomas in 2000	42
1961 and 1969 bomas degraded by 2000	2
New bomas $year^{-1}$, 1961–2000	1·15

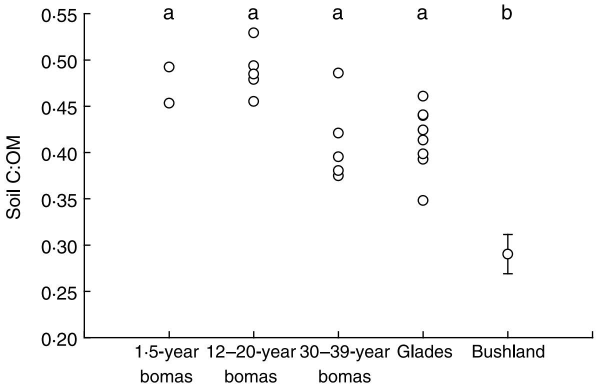


Fig. 1. Variation in soil C:OM ratios. For 1·5-year bomas, values are for the dung layer, which averages 13–15 cm in depth and was distinct from mineral soil. In all older bomas, dung was thoroughly mixed with mineral soil and separate layers could not be distinguished. Letters indicate differences among categories at the $P < 0{\cdot}05$ level.

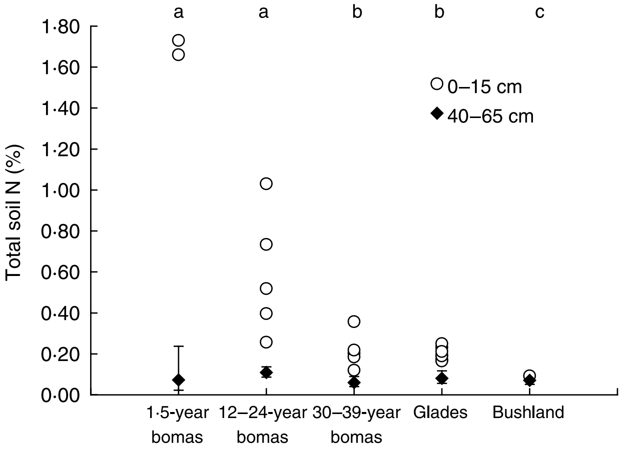


Fig. 2. Variation in total soil N. Data are geometric means for each boma or glade site (0–15 cm) or means across all sites in each category (40–65 cm). For bushland soils, only the geometric mean of all 46 sites sampled is shown; 95% confidence limits are smaller than the symbol. Letters indicate differences among categories at the $P < 0{\cdot}05$ level for 0–15-cm soils.

bomas were similar to ratios for soil from bomas abandoned 12–24 years ago (Fig. 1). Secondly, C:OM ratios for 30–39-year-old bomas were nearly identical to glades and lower than but statistically indistinguishable from younger bomas (Fig. 1). Finally, C:OM ratios for glade and abandoned boma soils were significantly different from bushland soils ($F_{4,61} = 20{\cdot}10$, $P < 0{\cdot}001$; Tukey HSD, $P < 0{\cdot}002$ for all four comparisons).

In contrast to organic matter quality, total N content in the surface soil layer (0–15 cm) declined dramatically from 1·5-year to 12–24-year to 30–39-year bomas (Fig. 2; $F_{4,69} = 39{\cdot}42$, $P < 0{\cdot}001$). Soil N in 30–39-year bomas was similar to glades (Tukey HSD, $P = 0{\cdot}99$), and mean glade concentrations were nearly double that observed for bushland soils (Tukey HSD, $P < 0{\cdot}001$; Fig. 2). In contrast, N in soils from 40–65-cm depth varied minimally among sites (Fig. 2). Concentrations beneath 12–24-year bomas were slightly greater than beneath 30–39-year bomas (Tukey HSD; $P = 0{\cdot}01$) but no other significant differences among site categories were detected.

Total P in soils from 0–15-cm depth also varied significantly among age categories (Fig. 3; $F_{4,69} = 46{\cdot}13$, $P < 0{\cdot}001$). However, two differences in patterns for soil N vs. P are noteworthy. First, mean N concentration in the dung layer of 1·5 year bomas was 7·2 times greater than the mean for all glades, while P concentrations in 1·5 year bomas were only 4·0 times greater than glades. Conversely, mean N concentration of glades was only 1·9 times greater than bushland soils, while P concentrations in glades were 7·4 times greater than bushland soils. In other words, soil N content declined more rapidly than soil P. Secondly, for 12–24-year bomas, 30–39-year bomas and glades, the among-site coefficient of variation for soil N was 52%, 40% and 16%, respectively, while the coefficient of variation for soil P was 46%, 81% and 43%, respectively, i.e. the decline in nutrients with age was more consistent for soil N than soil P (Fig. 2 vs. Fig. 3).

Despite this variation in soil nutrients, the texture of soils (mean percentage sand content ± 95% confidence interval) showed no major differences among glades (74·7 ± 4·8), old bomas (80·2 ± 2·7) and bushland sites (75·8 ± 1·4; $F_{2,56} = 2{\cdot}39$, $P = 0{\cdot}10$).

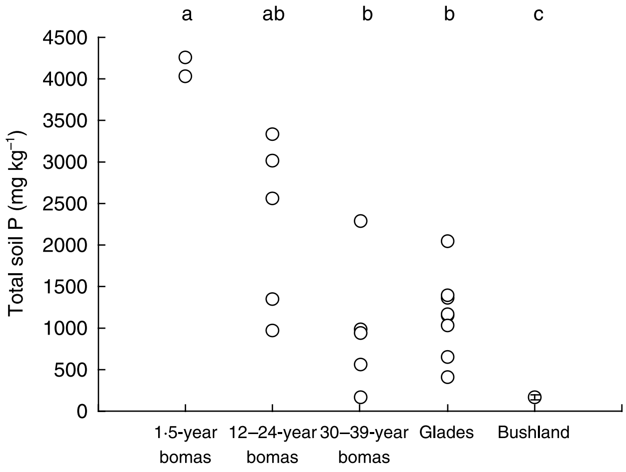


Fig. 3. Variation among sites in total soil P (mg kg^{-1}) for surface soils (0–15 cm). Symbols and statistics as in Fig. 2.

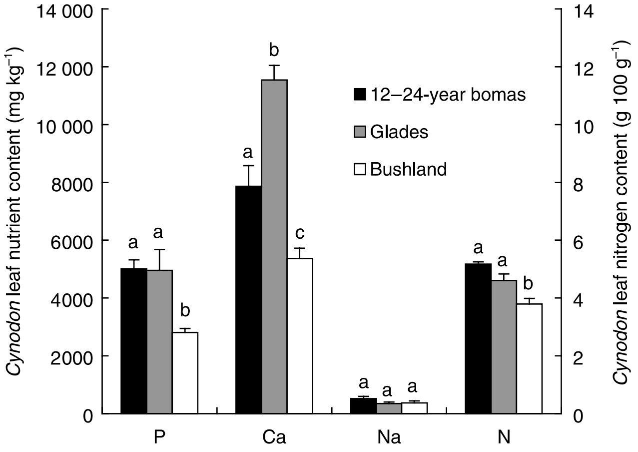


Fig. 4. Concentrations of P, Ca, Na and N in the youngest, fully expanded leaves (mean + 1 SE) of *Cynodon plectostachyus* at boma and glade sites and *Cynodon dactylon* at bushland sites. For each nutrient, different letters above the site categories indicate those categories differ significantly at the $P < 0{\cdot}05$ level.

GRASS NUTRIENT CONTENT

Cynodon leaf P, Ca and N content varied significantly among boma, glade and bushland sites ($F_{2,9} \geq 16{\cdot}88$, $P \leq 0{\cdot}001$; Fig. 4). No differences were observed for leaf Na content ($F_{2,9} = 2{\cdot}29$, $P = 0{\cdot}16$; Fig. 4). Leaf Ca content differed significantly among all three site categories and was greatest in glade *Cynodon* (Fig. 4). Leaf N and P concentrations were similar in glade and boma *Cynodon* but exceeded concentrations in bushland *Cynodon* (Fig. 4).

RELATIVE N LEACHING RATES

Two methods were used to examine the potential for N loss via leaching beneath abandoned bomas and glades. First, inorganic N concentrations varied significantly with depth ($F_{2,24} = 8{\cdot}52$, $P = 0{\cdot}002$) and among site categories ($F_{3,24} = 31{\cdot}09$, $P < 0{\cdot}001$), with no significant category by depth interaction ($F_{6,24} = 1{\cdot}02$, $P = 0{\cdot}43$). Concentrations were highly elevated beneath 1·5-year bomas and 12–24-year bomas for all soil depths relative to glade and bushland sites (Fig. 5). Although mean inorganic N levels were greater in the surface layer of glades relative to bushland, inorganic levels at greater depths were extremely low and nearly identical for these two communities. Most important, inorganic

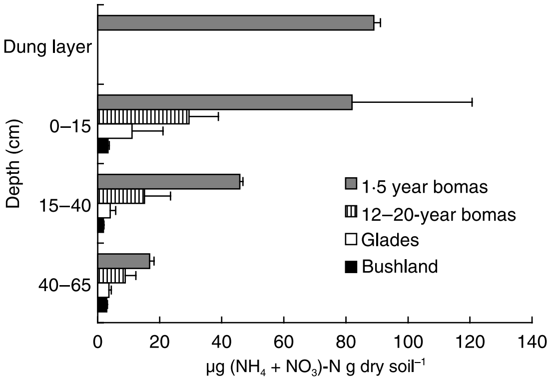


Fig. 5. Variation in KCl-extractable inorganic N concentrations (mean + 1 SE) among sites and by depth.

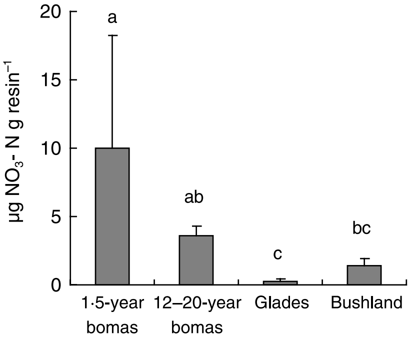
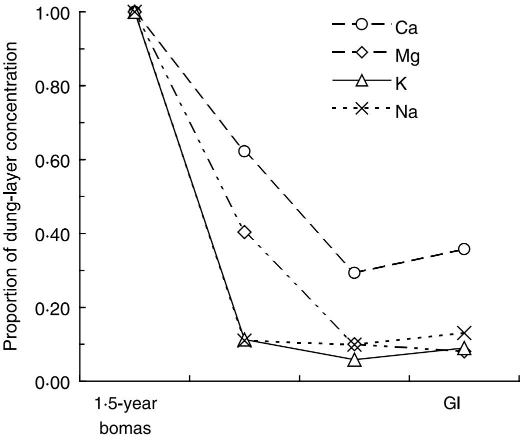


Fig. 6. Relative N-leaching rates (mean + 1 SE) based on NO_3-adsorption to ion-exchange resin bags buried at 65-cm depth.



N concentrations at 40–65 cm beneath 1·5- and 12–24-year bomas even exceeded the surface-layer concentrations in glades and bushland soils, respectively (Fig. 5). In dung, 0–15-cm and 15–40-cm layers, nitrate comprised 51%, 45% and 48% of total inorganic N, respectively, while at 40–65-cm depth nitrate comprised 71% of total inorganic N.

Secondly, measurements based on nitrate adsorption to ion-exchange resin bags buried at 65-cm depth showed significantly greater rates of N leaching beneath recently abandoned bomas relative to glades and bushland sites ($F_{3,7} = 12{\cdot}83$, $P = 0{\cdot}003$; Fig. 6). Nitrate adsorption was extremely low beneath glades and bushland sites. Mean relative leaching rate was also greater beneath 12–20-year bomas than glades and bushland, but was only statistically different from glades (Fig. 6).

SOIL CATION CONCENTRATIONS ALONG A BOMA–GLADE CHRONOSEQUENCE

Soil Ca, Mg, K and Na concentrations differed dramatically among the five site categories ($F_{4,69} > 16{\cdot}42$, $P < 0{\cdot}001$ for each cation; Table 2). If leaching is an important process leading to N and cation loss from abandoned bomas over time, then cations held more strongly to soil exchange sites are predicted to persist in boma soils longer than more weakly held cations. Relative loss rates are predicted to follow the sequence Na > K > Mg > Ca. When cation concentrations in older bomas and glades were evaluated relative to the dung layer of 1·5-year bomas, the pattern of cation concentration decline from 1·5-year bomas to 12–24-year bomas, 30–39-year bomas and glades matched the predicted pattern, with the exception that both Na and K declined to a similar degree after 12–24 years (Fig. 7).

BOMA N AND P INPUTS

The amount of N and P retained within the 1·5-year bomas averaged 827 g N m^{-2} and 230 g P m^{-2} (Table 3). These values are the difference in total N and P in the dung + 0–15-cm layer of the recently abandoned bomas vs. the 0–15-cm layer of an adjacent bushland site, and hence do not include nutrient losses that occurred between boma occupancy and 1·5 years after abandonment. Rates of P deposition into a 0·77-ha boma containing 360 cattle were also estimated based on measured rates of defecation and mean dung-group weight (Table 4). These measures, combined with wet- and dry-season P concentrations in dung (Table 4), predicted 42 months are required for 230 g P m^{-2} to be deposited into the boma (Fig. 8a). Herders report that one of the sampled bomas was constructed in 1993 and abandoned in late 1997, but the site was occupied intermittently and hence the exact number of months that cattle were present is unknown. Given the same measures and assumptions for N deposition in dung (Table 4), only 31·5 months are required for predicted cumulative deposition to meet the amount of N

Table 2. Geometric means (1 SE) for total soil Ca, Mg, K and Na (mg kg^{-1} dry soil). Letters indicate significant differences among categories at the $P < 0{\cdot}05$ level

Category	Ca	Mg	K	Na
1·5 year bomas	10021 (449)a	7331 (505)a	16446 (341)a	453 (87)a
12–24 year bomas	6238 (1062)a	2958 (945)a	1862 (377)b	50 (6)b
30–39 year bomas	2939 (837)a	736 (351)b	956 (165)cd	45 (6)b
Glades	3585 (438)a	590 (62)b	1480 (162)c	59 (7)b
Bushland	958 (91)b	252 (17)c	736 (42)d	49 (3)b

Table 3. Amounts of N and P contained within two bomas abandoned 1·5 years prior to sampling and at paired bushland sites

	Boma	Bushland	Difference
g N m^{-2}			
Site 1			
Dung layer	701		
0–15-cm soil	163	191	673
Site 2			
Dung layer	883		
0–15-cm soil	260	161	982
g P m^{-2}			
Site 1			
Dung layer	183		
0–15-cm soil	44	19	208
Site 2			
Dung layer	220		
0–15-cm soil	53	21	252

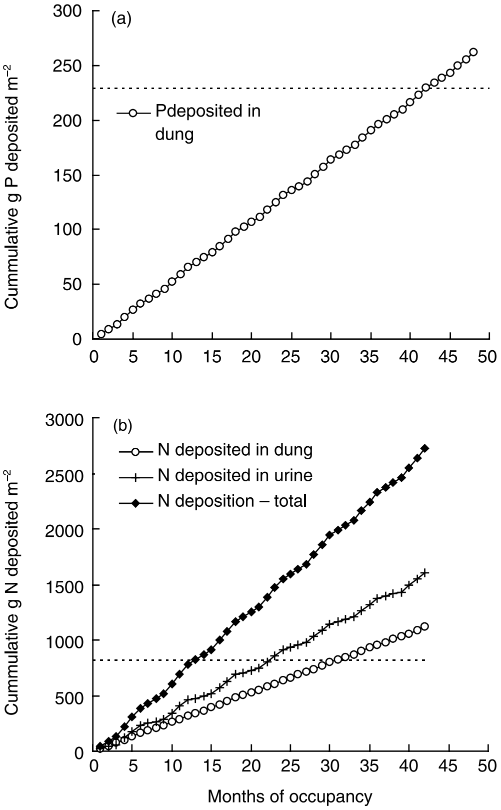


Fig. 8. Predicted rates of N and P accumulation in a boma. Dashed lines show the mean amount of P and N measured within two bomas abandoned 1·5 years ago, after correcting for P and N occurring naturally in nearby bushland sites (Table 3). Predicted P accumulation matches measured amounts after 42 months (a), but predicted N accumulation matches measured amounts after only 13 months (b).

measured 1·5 years after occupancy (Fig. 8b). Furthermore, once estimates of urine deposition are included, only 13 months are required to meet the observed deposition (Fig. 8b).

Because N can be lost rapidly via volatilization and leaching after boma abandonment, while P is biogeochemically much more stable, the P concentrations measured 1·5 years after abandonment were used to estimate that the bomas were occupied for 42 months. During this time, 2721 g N m^{-2} were predicted to have been deposited into the boma in dung and urine, which exceeded the amount observed 1·5 years later by 1894 g N m^{-2}.

This estimated N deposition into bomas, which corresponds to 20 944 kg total deposition for a 7700-m^2 boma, must be removed from the surrounding grazed rangeland. Amounts removed from the rangeland on an areal basis depend on the total area grazed, with removal estimates declining from 2·1 g N m^{-2} for 10 km^2 of rangeland to 0·70 g N m^{-2} for 30 km^2 of rangeland.

Table 4. Measured and derived variables used to predict deposition rates of N and P into a boma as a function of length of boma occupancy (Fig. 8)

Measured variables	Units	Mean	1 SE
Mean dung group weight	g group^{-1}	242·6	11·7
Groups excreted 12 h^{-1}	groups 12 h^{-1}	6·5	0·44
No. cattle in boma	Number	360	
Size of boma	m^2	7700	
Dung-N, dry season	% dry weight	1·09	0·04
Dung-N, wet season	% dry weight	1·32	0·03
Dung-P, dry season	% dry weight	0·198	0·020
Dung-P, wet season	% dry weight	0·297	0·017
Derived variables			
g excreted 12 h^{-1} cow^{-1}		1576·9	
g excreted 12 h^{-1} m^{-2}		73·7	
g dung-N excreted 12 h^{-1} m^{-2}: dry season		0·802	
g dung-N excreted 12 h^{-1} m^{-2}: wet season		0·973	
g P excreted 12 h^{-1} m^{-2}: dry season		0·146	
g P excreted 12 h^{-1} m^{-2}: wet season		0·219	
Predicted, dry season			
g urine-N excreted 12 h^{-1} m^{-2}		0·658	
Predicted, wet season			
g urine-N excreted 12 h^{-1} m^{-2}		1·887	

Corresponding estimates for P vary from 0·19 g P m^{-2} for 10 km^{-2} of rangeland to 0·06 g P m^{-2} for 30 km^{2} of rangeland. For comparison, the rate of N deposition in rainfall over 7 months in 1999 was 0·25 g N m^{-2}, which corresponds to 0·46 g N 500 mm rainfall^{-1} or 0·43 g N year^{-1}.

Discussion

ORIGINS OF NUTRIENT-ENRICHED GLADES

Six lines of evidence are consistent with the hypothesis that long-term glades are derived from abandoned cattle bomas. First, the quality of organic matter in glades, as measured by C:OM ratios, is similar to old bomas but distinctly different from bushland soils. Observed ratios are clearly consistent with the hypothesis that organic matter in glade soils was originally derived from manure. Secondly, N concentrations in the surface (0–15 cm) layer of glade soils are similar to those in 30–39-year bomas and significantly greater than bushland soils, while N in soils from 40–65-cm depth was similar across all 30–39-year bomas, glades and bushland sites. This pattern is inconsistent with the hypothesis that glades occur on soils derived from a localized nutrient-enriched parent material. Thirdly, P in glade surface soils was similar to levels both in 12–24-year and 30–39-year bomas, but more than seven times greater than bushland soils. Fourthly, the relative decline in soil Na, K, Mg and Ca across the boma and glade site categories is consistent with expected rates if these categories represent a chronosequence of sites with increasing age. It is worth noting that results also suggest soil Mg:Ca ratios may be a particularly useful indicator of boma age. Fifthly, as discussed by Young, Partridge & Macrae (1995), glades are often located at upper topographic positions along a ridge or at the base of granitic inselburgs, similar to sites of Maasai settlements in southern Kenya (Western & Dunne 1979).

Finally, the similarity in soil texture between glades and bushland is clearly consistent with the hypothesis that glade and bushland soils have the same geological origin but glades have been fertilized by manure. Termite activities could potentially create nutrient-enriched patches such as glades, but on sandy soils such as in this study termite mounds have much larger fractions of silt and clay than the surrounding soil type (Lee & Wood 1971; Konate *et al.* 1999). Similarly, a difference in soil texture would be expected if glades were created by weathering of small pockets of parent material that differ from the parent material of surrounding bushland soil (Blackmore, Mentis & Scholes 1990).

Despite clear evidence that glades are derived from abandoned bomas, several observations suggest boma construction and use patterns have changed since European settlement. The mean size of abandoned bomas is less than the mean glade size (Table 1), which may reflect differences in customs of ranch managers vs. Maasai pastoralists and variation in livestock numbers and species present in recent decades. However, bomas abandoned in the past 5 years, each known to have contained *c.* 360 cattle, still averaged 0·69 ha in size, similar to the size of long-term glades. Maasai settlements typically contain both human dwellings and livestock within an outer thorn scrub enclosure (Homewood & Rodgers 1991), such that glades are likely to receive inputs from cooking fires and decomposing dwellings, in addition to the primary input from manure. Currently at MRC, dwellings of herders (primarily Turkana) are located outside the cattle enclosure, and cooking fires represent an additional pathway of nutrient accumulation around the boma periphery. Glades are also devoid of shrubs, while 53% of bomas abandoned after 1961 contained mature shrubs growing along the former fence lines. This difference may reflect an increase in firewood availability over time, the loss of fence-line shrubs from glades due to eventual mortality combined with a lack of shrub recruitment, or differences in customs of Maasai vs. current ranch herders.

High rates of boma abandonment during 1961–2000 combined with a lack of glade disappearance (Table 1) suggest boma relocation rates have changed from pre- vs. post-European settlement periods. Clearly, if these same rates applied to the century prior to European settlement, glades should cover far more than 0·5% of the landscape. Increases in livestock numbers this century are a possible explanation, but stocking rates on MRC and other commercial ranches are typically far lower than rates on pastoral rangeland. A second possibility is that Maasai bomas were used for longer periods and reused more often, such that new bomas were created less frequently in the previous century. A third possibility is that mechanisms maintaining glades in a nutrient-enriched state, such as preferential use and hence nutrient inputs by ungulate herbivores (Blackmore, Mentis & Scholes 1990), have increased in importance this century. Finally, the presence of *Pennisetum mezianum* and bare soil patches in three glades indicates that long-term deterioration to bushland vegetation does occur over time scales greater than 40 years. In addition, two small bomas in the 1961 aerial photos were indistinguishable from bushland vegetation by 2000. Their disappearance suggests at least a minimum threshold of manure input may be necessary for glade development.

CATTLE BOMAS AND LANDSCAPE-LEVEL N AND P DISTRIBUTION

This study highlights two conflicting effects that cattle bomas exert on savanna ecosystems. First, abandoned bomas create nutrient-enriched patches within the landscape that support plant communities with mineral-rich grasses. Although these patches cover only 1% of the landscape, the intensive use of glades and bomas by native ungulates (Young, Partridge & Macrae 1995) indicates they are far more important to herbivore populations than their frequency within the landscape suggests. Both cattle and wildlife can clearly benefit from the levels of P, Ca and N in glade and boma grasses, which are sufficient to supply amounts recommended for lactation and pregnancy in cattle (McDowell 1985) and wild ruminants (Robbins 1993). Levels of P and Ca in glade forage are also similar to those observed in grasslands supporting high concentrations of resident ungulates in the Serengeti ecosystem, where hotspots of P- and Ca-enriched forage appear to be a critical ungulate habitat component (McNaughton 1988). Concentrations of P in *Cynodon* growing on bushland soils were lower than the recommended levels of 4000–6000 mg kg^{-1} for lactating and pregnant cattle (McDowell 1985), again suggesting that spatial heterogeneity created by bomas improves herbivore carrying capacity by providing patches of P-sufficient forage. Furthermore, on many managed rangelands the maintenance of native wildlife populations for tourism or hunting is an important consideration. Current boma locations could therefore be managed with an aim to create wildlife hot spots in desired locations for decades after boma abandonment. From the perspective of large herbivores, the only nutrient still deficient in glade and boma grasses was Na. How native ungulates meet dietary Na requirements at MRC remains unclear.

Second, although nutrient-enriched glades can clearly benefit large herbivores, the nutrients in bomas are removed from the surrounding landscape with a potential cost to the bushland community. The analysis of N and P deposition and retention in bomas indicates that they create greater heterogeneity in soil P than in soil N across the landscape. P is likely to be highly conserved in bomas because losses via leaching and gaseous forms are minimal or non-existent and inorganic P often immediately complexes with soil minerals; long-term losses occur primarily in surface run-off (Schlesinger 1997). In this study, when P deposition estimates were used to calculate the occupancy time for recently abandoned bomas (Fig. 8a), corresponding N deposition and retention estimates indicated 70% of total N deposition is lost within 1·5 years of abandonment (Fig. 8b). Such a massive rate of N loss is consistent with measured NH_3 volatilization rates of 0·33–4·15 g N m^{-2} day^{-1} from feedlot manure (Sommer *et al.* 1996) and with studies of N vs. P loss from cattle feedlots in the USA. For example, manure composted over 110 days lost 19–42% of the initial N content, primarily via volatilization, while losing only 0·8% of the total P (Eghball *et al.* 1997).

The pathway of N loss from bomas has significant implications for the effect of livestock on N cycling at the landscape level. Measured relative N-leaching rates indicate at least a small proportion of boma N is lost permanently from the ecosystem. This loss continues at a greater rate in bomas relative to long-term glades and bushland communities until 12–24 years after abandonment (Fig. 5). Changes in the concentration of soil Na, K, Mg and Ca also indicate that nutrients are leached from the surface soil layer over the first 24 years after abandonment. However, leaching losses occur over a small absolute area and for N probably represent a small proportion of total N lost from the boma. Studies of feedlot manure decomposition showed that 92% of N was lost via NH_3 volatilization while only 0·5% was lost as ammonia and nitrate in leachate (Eghball *et al.* 1997). These findings suggest volatilization as the primary pathway for boma N loss, but the absolute magnitude of permanent losses due to leaching and denitrification are still uncertain.

NH_3 volatilization from bomas may not represent a permanent ecosystem loss because this N is returned to the landscape in rainfall. Because the district of Laikipia is primarily engaged in livestock production and nearly all ranches use bomas, the direction of prevailing winds may not affect N loss for ranches such as MRC located in the centre of the district. In addition, most precipitation occurs as local convective storms that are unlikely to transport volatilized N long distances. Thus, a redistribution rather than permanent loss of N seems likely. N deposition in rainfall at MRC in 1999 was 0·43 g m^{-2} year^{-1}. At MRC, the area grazed by cattle from a given boma is typically within the range 20–25 km^2, which corresponds to N removal rates of 0·8–1·1 g m^{-2} over the entire period of boma occupancy, or 0·24–0·30 g N m^{-2} year^{-1}. Thus, N inputs from rainfall are more than sufficient to replace losses from the grazed rangeland due to bomas. Furthermore, this estimated input does not include dry deposition or plant uptake of HNO_3 gas (Schlesinger 1997). Other potential, but unmeasured, N inputs to bushland soils include N-fixation by symbiotic bacteria associated with *Acacia* and *Indigofera* plants, by lichens that cover many dead shrub branches, and by cyanobacteria in soil crusts. These calculations therefore support the conclusion that most boma N loss occurs via volatilization and is redistributed across the landscape. The fact that 60% of rainfall N at MRC consisted of NH_4^+, which is far higher than the 13% NH_4^+-N reported in rainfall where fossil fuel burning is the main source (Likens & Bormann 1995), also indicates most rainfall N is derived from volatilization. However, it is important to note that cattle grazing pressure is often distributed unevenly across landscapes (Senft *et al.* 1987) while N deposition in rainfall is relatively uniform. As a result, N removal from the bushland by cattle may be accentuated near bomas and in favoured grazing areas, and further work is needed to address the implications of heterogeneous grazing and N removal for long-term rangeland stability.

Management of cattle via bomas creates a particularly heterogeneous distribution of P across the landscape, with deposition into bomas removing an estimated 0·021–0·026 g P m^{-2} year^{-1} from grazed rangeland. Redistribution of P by cattle has been reported at scales of up to 5 km radii from heavily used watering points (Turner 1998a) and the reduction in P availability at sites distant from cattle foci can reduce rangeland productivity after long dry seasons (Turner 1998b). P loss due to deposition in bomas could therefore reduce bushland productivity in some years, while creating small, highly productive sites supporting P-rich forage for decades after boma abandonment. This change in the spatial distribution of P can benefit native and domestic ungulate herbivores by providing unique habitats where requirements for mineral nutrients can be met during the growing season (McNaughton 1988; Ben-Shahar & Coe 1992; Seagle & McNaughton 1992).

Overall, this study highlights the major effect that cattle management via bomas exerts on the distribution of soil and plant nutrients at the landscape level. Because the primary focus of boma use is to prevent cattle theft and predation, rangeland managers rarely consider the long-term implications for savanna productivity and forage nutritional sufficiency. Such considerations should be especially important for nutrient-poor savannas with soils derived from basement complex materials. Results of this study indicate that, under current practices, significant quantities of N (Fig. 1) and a lesser amount of P (Fig. 2) deposited in bomas are lost during the decades leading to glade formation. In other words, the amounts of nutrients deposited into bomas are typically far in excess of the amounts found in glade soils, which nevertheless are sufficient to support highly nutrient-enriched grasses. As a result, managers could increase the availability of nutrient-enriched patches on the landscape by increasing boma rotation and abandonment rates, as constrained by construction costs and other cattle management needs. Conversely, factors such as increased sedentarization of pastoralists, the use of permanent bomas that more effectively deter predators, and the use of relatively permanent bomas around water sources and cattle dips will create a nutrient drain on the ecosystem by concentrating manure into a smaller area of the landscape and reducing opportunities for long-term glade development.

Acknowledgements

I thank F. Lomojo, J. Ekiru and D. M. Augustine for assistance and enthusiasm with field data collection, M. McNaughton for assistance with laboratory analyses, and the Office of the President of the Republic of Kenya for permission to conduct research in Kenya. N. J. Georgiadis, S. J. McNaughton, T. P. Young, D. A. Frank, C. Johnson, M. J. Mitchell and L.L. Wolf provided many helpful comments on this paper. Financial support was provided by the National Geographic Society, an NSF predoctoral fellowship to D. J. Augustine, and NSF grant DEB-9813050 to S. J. McNaughton.

References

Ahn, P.M. & Geiger, L.C. (1987) *Kenya Soil Survey – Soils of Laikipia District*. Ministry of Agriculture, National Agricultural Laboratories, Kabete, Kenya.

Behnke, R., Scoones, I. & Kerven, C. (1993) *Range Ecology at Disequilibrium*. Overseas Development Institute, London, UK.

Ben-Shahar, R. & Coe, M. (1992) The relationships between soil factors, grass nutrients and the foraging behaviour of wildebeest and zebra. *Oecologia*, **90**, 422–428.

Binkley, D. (1984) Ion exchange resin bags: factors affecting estimates of nitrogen availability. *Soil Science Society of America Journal*, **48**, 1181–1184.

Blackmore, A.C., Mentis, M.T. & Scholes, R.J. (1990) The origin and extent of nutrient-enriched patches within a nutrient-poor savanna in South Africa. *Journal of Biogeography*, **17**, 463–470.

Blundell, M. (1987) *Wild flowers of East Africa*. William Collins Sons & Co., London, UK.

Eghball, B., Power, J.F., Gilley, J.E. & Doran, J.W. (1997) Nutrient, carbon and mass loss during composting of beef cattle feedlot manure. *Journal of Environmental Quality*, **26**, 189–193.

Fynn, R. & O'Connor, T. (2000) Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in a semi-arid savanna, South Africa. *Journal of Applied Ecology*, **37**, 491–507.

Homewood, K.M. & Rodgers, W.A. (1991) *Maasailand Ecology: Pastoralist Development and Wildlife Conservation in Ngorongoro, Tanzania*. Cambridge University Press, Cambridge, UK.

Huntington, T., Johnson, C., Johnson, A., Siccama, T. & Ryan, D. (1989) Carbon, organic matter, and bulk density relationships in a forested spodosol. *Soil Science*, **148**, 380–386.

Illius, A. & O'Connor, T. (1999) On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications*, **9**, 798–813.

Johnson, C. (1995) Soil nitrogen status 8 years after whole-tree clear-cutting. *Canadian Journal of Forest Research*, **25**, 1346–1355.

Keya, N. (1973) The effect of NP fertilizers on the productivity of *Hypharrenia* grassland. *East African Agricultural and Forestry Journal*, **39**, 195–200.

Kingdon, J. (1997) *The Kingdon Field Guide to African Mammals*. Academic Press, London, UK.

Konate, S., Le Roux, X., Tessier, D. & Lepage, M. (1999) Influence of large termitaria on soil characteristics, soil water regime, and tree leaf shedding pattern in a West African savanna. *Plant and Soil*, **206**, 47–60.

Lee, K.E. & Wood, T.G. (1971) *Termites and Soils*. Academic Press, London, UK.

Likens, G.E. & Bormann, F.H. (1995) *Biogeochemistry of a Forested Ecosystem*, 2nd edn. Springer-Verlag, New York, NY.

McDowell, L.R. (1985) *Nutrition of Grazing Ruminants in Warm Climates*. Academic Press, New York, NY.

McNaughton, S.J. (1988) Mineral nutrition and spatial concentrations of African ungulates. *Nature*, **334**, 343–345.

O'Connor, T.G. (1985) *A Synthesis of Field Experiments Concerning the Grass Layer in the Savanna Regions of Southern Africa*. South African National Science Programme, Pretoria, South Africa.

Polhill, R.M. (1972) *Flora of Tropical East Africa, Gramineae. Part 1*. Whitefriars Press, London, UK.

Polhill, R.M. (1974) *Flora of Tropical East Africa, Gramineae. Part 2*. Whitefriars Press, London, UK.

Polhill, R.M. (1982) *Flora of Tropical East Africa, Gramineae. Part 3*. A. A. Balkema, Rotterdam, the Netherlands.

Reid, R.S. & Ellis, J.E. (1995) Impacts of pastoralists on woodlands in south Turkana, Kenya: livestock-mediated tree recruitment. *Ecological Applications*, **5**, 978–992.

Rice, J. & MacCarthy, P. (1991) Statistical evaluation of the elemental composition of humic substances. *Organic Geochemistry*, **17**, 635–648.

Robbins, C.T. (1993) *Wildlife Feeding and Nutrition*. Academic Press, New York, NY.

Schlesinger, W.H. (1997) *Biogeochemistry*. Academic Press, New York, NY.

Scholefield, D., Lockyer, D.R., Whitehead, D.C. & Tyson, K.C. (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. & McNaughton, S.J. (1992) Spatial variation in forage nutrient concentrations and the distribution of Serengeti grazing ungulates. *Landscape Ecology*, **7**, 229–241.

Senft, R.L., Coughenour, M.B., Bailey, D.W. & Rittenhouse, L.R. (1987) Large herbivore foraging and ecological hierarchies. *Bioscience*, **37**, 789–799.

Sommer, S.G., Sibbesen, E., Nielsen, T., Schjorring, J.K. & Olesen, J.E. (1996) A passive flux sampler for measuring ammonia volatilization from manure storage facilities. *Journal of Environmental Quality*, **25**, 241–247.

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. (1998a) Long-term effects of daily grazing orbits on nutrient availability in Sahelian West Africa. I. Gradients in the chemical composition of rangeland soils and vegetation. *Journal of Biogeography*, **25**, 669–682.

Turner, M.D. (1998b) Long-term effects of daily grazing orbits on nutrient availability in Sahelian West Africa. II. Effects of a phosphorus gradient on spatial patterns of annual grassland production. *Journal of Biogeography*, **25**, 683–694.

Weber, G., Jeltsch, F., van Rooyen, N. & Milton, S. (1998) Simulated long-term vegetation response to grazing heterogeneity in semi-arid rangelands. *Journal of Applied Ecology*, **35**, 687–699.

Western, D. & Dunne, T. (1979) Environmental aspects of settlement site decisions among pastoral Maasai. *Human Ecology*, **7**, 131–145.

Young, T.P., Partridge, N. & Macrae, A. (1995) Long-term glades in acacia bushland and their edge effects in Laikipia, Kenya. *Ecological Applications*, **5**, 97–108.

Received 16 October 2001; final copy received 13 September 2002