ECOSYSTEMS

N and P Cycling in Tanzanian Humid Savanna: Influence of Herbivores, Fire, and N₂-Fixation

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ABSTRACT

Availabilities of nitrogen (N) and phosphorus (P) have a strong influence on plant growth and the species composition of savannas, but it is not clear how these availabilities depend on factors such as fire, N₂-fixation, and activities of wild herbivores and cattle. We quantified soil N and P availabilities in various ways (extractable pools, mineralization, resin adsorption) along vegetation gradients within a recently abandoned cattle ranch and a former game reserve in Tanzania (both areas now part of the Saadani National Park). We also assessed annual N and P balances to evaluate how long-term availabilities of N and P are affected by large herbivores, symbiotic N₂-fixation, and fire. The results show that cattle ranching led to a spatial re-distribution of nutrients, with the local accumulation of P being stronger and more persistent than that of N. In the former game reserve, intensively grazed patches of short grass tended to have elevated soil N and P availabilities; however, because quantities of nutrients removed through grazing exceeded returns in dung and urine, the nutrient balances of these patches were negative. In dense *Acacia* stands, N₂-fixation increased N availability and caused a net annual N input. Fire was the major cause for nutrient losses from tallgrass savanna, and estimated N inputs from the atmosphere and symbiotic N₂-fixation were insufficient to compensate for these losses. Our results call into question the common assumption that N budgets in annually burned savanna are balanced; rather, these ecosystems are a mosaic of patches with both N enrichment and impoverishment, which vary according to the vegetation type.

Key words: fire; herbivory; N-fixation; N:P stoichiometry; nutrient balances; mineralization.

INTRODUCTION

Savannas are tropical ecosystems co-dominated by trees and grasses that occur in regions with strongly seasonal rainfall. In most savannas, plant growth is limited not only by lack of water but also by shortages of nitrogen and/or phosphorus (Medina 1987; Cech and others 2008; Craine and others 2008). Factors including fire, herbivores (both native and domestic), and N₂-fixation (McNaughton and others 1997; Augustine 2003; Fynn and others

2003; Ludwig and others 2004) influence the availabilities and spatial distributions of these nutrients, but their relative importance remains largely unknown.

Human activities have a considerable influence upon both the frequency and the extent of fires in African savannas, with fire frequency being generally higher in regions with a high human population (Stott 2000; Bond and others 2005; Archibald and others 2009). In some national parks, fire is used as a management tool to attract animals and increase visibility of wildlife (Eriksen 2007). Data from long-term fire experiments in tallgrass prairies and savannas indicate that recurrent fires over long periods lead to a reduction in nitrogen mineralization and total soil N pools (Ojima and others 1994; Reich and others 2001; Fynn and others 2003; Buis and others 2009), although such a decline is not always observed (Aranibar and others 2003b; Coetsee and others 2008). Data on the effect of fire on soil phosphorus availability and mineralization in savannas are scarce, but there is evidence that levels of extractable P are higher in annually burned savannas than in nearby protected sites (Harrington 1974; Brookman-Amissah and others 1980; Singh and others 1991).

The effect of herbivory on nutrient availability is known to vary spatially and among animal species. Some large herbivores re-distribute nutrients by feeding in certain areas while depositing their excreta in others (Edwards and Hollis 1982; Jewell and others 2007), thus causing local depletion or enrichment of nutrients. In contrast, others feed and return their excreta in the same, intensively used areas, thereby maintaining nutrient-rich patches in otherwise nutrient-poor vegetation (Lamoot and others 2004). For tallgrass prairie, it has been shown that grazers reduce the biomass consumed in fires, and thereby have a positive effect upon the nitrogen balance (Hobbs and others 1991). The net effect of herbivores on soil N turnover, however, is less consistent: N mineralization was increased by bison in Yellowstone National Park and by prairie dogs in the South Dakota mixed grass prairie (Holland and Detling 1990; Frank and Groffman 1998), but was decreased by cattle in North Dakota rangelands and Kenyan semi-arid savanna (Biondini and others 1998; Augustine and McNaughton 2006). In Serengeti, McNaughton and others (1997) found lower N mineralization rates at sites with few resident native herbivores than at sites with many, but could not determine whether this was due to the differences in herbivore activity. We are unaware of any quantitative studies in tropical savannas of the relative effects of wild and domestic herbivores upon nutrient availability and cycling, though such information would be useful for assessing the impacts of intensified livestock production (Kauffman and others 1995; Scholes and Archer 1997; Augustine and others 2003).

Woody legumes, especially of the genus *Acacia*, are conspicuous elements of many savannas, and their abundance and distribution are significantly influenced by livestock grazing (Hudak 1999; Tobler and others 2003). Partly due to their capacity to fix atmospheric N_2, more nitrogen accumulates and is mineralized beneath leguminous trees and shrubs than in open grassland (Geesing and others 2000; Ludwig and others 2004). Several authors have suggested that the N gained by symbiotic fixation compensates for N lost due to fire (Medina and Bilbao 1991; Sanhueza and Crutzen 1998; Laclau and others 2005), though this has not been explicitly investigated.

Most studies of nitrogen availability in tropical savannas have focussed on the effects of either fire or herbivory, and data on the influence of other factors are scarce. And there is even less information on the factors affecting phosphorus availability, despite the importance of this nutrient for plant growth (Cech and others 2008). The aim of this study is to compare the influence of domestic and wild herbivores upon soil nutrient conditions in a humid coastal savanna in Tanzania. To do this, we investigated the availabilities and main fluxes of nitrogen and phosphorus along vegetation gradients in a recently abandoned cattle ranch and a neighboring game reserve (Figure 1). Our working hypotheses are presented diagrammatically in Figure 2. In the former ranch area, we expected the nutrient availabilities to be highest within and around the former paddocks where cattle were herded overnight, and to be lowest in pasture areas. Because N is lost through ammonia volatilization from dung and urine as well as from leaching (Ruess and McNaughton 1988; Frank and Zhang 1997; Augustine 2003), we expected nutrient enrichment due to cattle excreta to be more pronounced for P than for N. And because most *Acacia* species are known to fix atmospheric N_2 symbiotically (DeFaria and others 1989), we expected N availability to be higher in areas of bush encroachment than elsewhere. Regarding the effects of wild ungulates, we expected to find some N and P enrichment at heavily grazed sites, though less than for areas used by cattle.
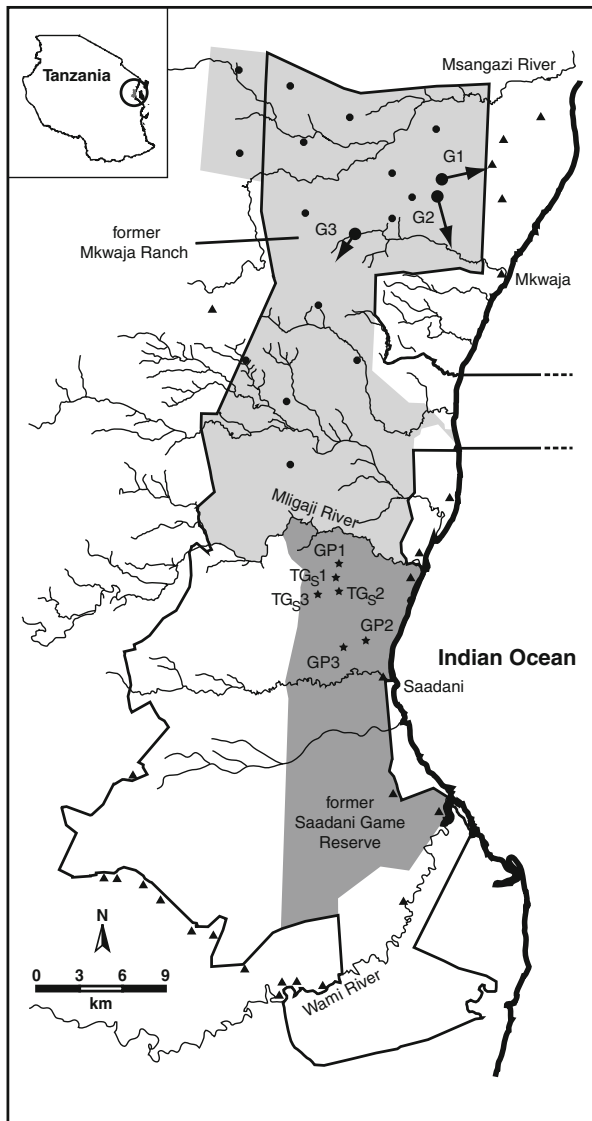
Figure 1. Map of Saadani National Park on the Tanzanian coast. The former Mkwaja ranch and the former Saadani Game Reserve are indicated by the *light gray* and *dark areas*, respectively. *Filled circles* indicate the location of former paddocks where cattle were herded overnight, *filled triangles* are villages. The three selected paddock gradients are indicated with *arrows*. The three grazed sites (GP) and the three tallgrass sites (TG$_S$) in the former game reserve are indicated with *stars*.

METHODS

Study Area

The study was conducted in the Saadani National Park on the Tanzanian coast (5° 43′ S, 38° 47′ E). The soils in this area are relatively nutrient-poor and consist of grayish fine sand or loamy sand in the flats, and reddish loamy sand over clay on slopes and hilltops (Klötzli 1980). Between 1954
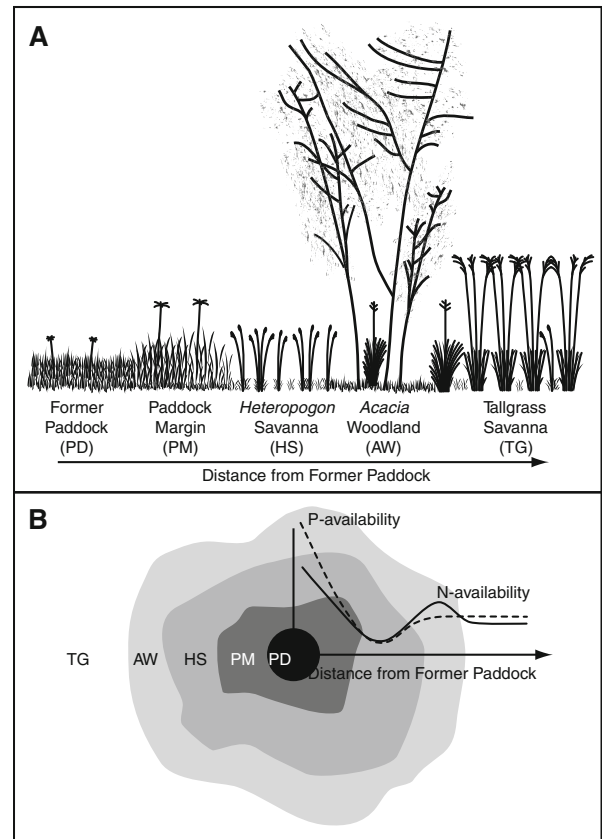

Figure 2. Schematic cross-section of the vegetation types found along paddock gradients in the former Mkwaja ranch area (**A**), and the expected patterns in relative N and P availabilities along the vegetation gradients (**B**).

and 2000, the northern half was used for cattle ranching, and supported up to 13,000 head of cattle on an area of approximately 460 km^2 (Figure 1). This grazing density of about 0.3 head/ha was about the maximum that this oligotrophic area could support, and is 2–4 times higher than the density reported by Augustine (2003) for a similar cattle ranch in Kenya. From 1969, much of the southern part was managed as a game reserve (Figure 1). Wild herbivores include warthog, waterbuck, reedbuck, buffalo, wildebeest, giraffe, and elephant, which continue to be much more abundant in the southern part than in the former ranch (Treydte and others 2005). Mean annual temperature recorded at the former ranch complex was 25°C (1973–1998). Annual precipitation from 1957 to 1998 ranged from 610 to 1700 mm, with a mean of 1040 mm. The wet season lasts from March until June, and there is a short rainy season from mid-October to mid-November. The driest months are January and February and August and September, and during these periods fires are common, many

of them being started deliberately by local people or by the park management. For a more detailed description of the study area see Tobler and others (2003).

The vegetation of the area is dominated mainly by bushland and grassland, but there are areas of evergreen forest. During the operation of the ranch, cattle were kept in paddocks with up to 1,500 animals at night, and during the day were driven to pasture areas and dams in herds of 200–400 animals. The effect of this management is still clearly reflected in the vegetation, with five concentric vegetation zones around each former paddock (Tobler and others 2003) (Figure 2): (1) the former paddocks (PD) are dominated by the stoloniferous grass *Cynodon dactylon*, which forms dense mats; (2) the margins of former paddocks (PM) are characterized by the grasses *Digitaria milanjiana*, *Eragrostis superba* and the sedge *Cyperus bulbipes*, reaching a height of 50–60 cm; (3) *Heteropogon* savanna (HS) is dominated by the grass *Heteropogon contortus*, accompanied by *Panicum infestum*, *Bothriochloa bladhii*, and the sedge *Abildgaardia triflora*, and reaching 60 cm; (4) *Acacia* woodlands (AW) are dominated by *Acacia zanzibarica* reaching heights up to approximately 8 m—*Panicum infestum*, *Heteropogon contortus*, and *Abildgaardia triflora* are most abundant in the herbaceous layer; (5) tallgrass savanna (TG_M) is dominated by the tall grasses *Hyperthelia dissoluta* and *Diheteropogon amplectens* with culms up to about 2 m height.

For our study we selected three former paddock systems (Figures 1, 2). Along each paddock gradient we selected five locations representative of the five vegetation types; the main criteria for selecting these locations were distance to the former paddock and species composition, but we also looked for homogenous sites without termite mounds. In the former game reserve, we selected three grazed patches (GP), sensu Archibald and others (2005). Field observations suggest that such patches are not grazed continuously, but are abandoned if the grass grows above a certain height; after that, they are not grazed again until the biomass is removed by fire. The lawn sites selected were dominated by the grasses *Panicum infestum*, *Heteropogon contortus*, *Digitaria milanjiana*, *Bothriochloa bladhii*, and the sedge *Bulbostylis pilosa*; the vegetation was approximately 7 cm tall and showed clear signs of intensive grazing. As reference sites with a low impact of native herbivores, we selected three nearby tallgrass sites dominated by the tall grasses *Hyperthelia dissoluta* and *Diheteropogon amplectens* (TG_S, Figure 1).

We monitored rainfall, temperature, and relative humidity during the study period at two locations—one in the northern and one the southern part of the national park—where we installed tipping bucket rain gauges and data loggers (HOBO RG3-M, HOBO H8 Pro, Onset Computer Corp., Bourne, Massachusetts, USA).

Measurement of Nutrient Pools and Soil Turnover Rates

Aboveground herbaceous biomass was determined at all sites at the beginning of the dry season in July 2005. Additionally, total herbaceous biomass (that is, including root biomass) was determined for four vegetation types (PM, AW, TG_M, and GP) after the short wet season in January 2007. At each site aboveground biomass was measured by clipping four 50×50 cm^2 per site at ground level. To measure belowground biomass, four soil cores (4.2 cm diameter, 20 cm depth) were extracted from each of the clipped squares and pooled. Soil was sieved (2 mm) and root biomass collected separately from rhizomes/shoot bases. By reference to other studies, we assume that our coring method sampled most of the belowground biomass; for example, McNaughton and others (1998) found that the upper 20 cm of soil in mid-height and tall grasslands in Serengeti (comparable to our herbaceous layer) contained at least 78% of the total belowground biomass. Harvested biomass was dried to constant weight and, after Kjeldahl digestion, analyzed for total N and P content by means of a continuous flow injection analyzer (FIAStar, Foss Tecator, Höganäs, Sweden). Additionally, we determined the biomass production of the regrowth in the clipped squares after approximately 100 days in early November, and again in late December 2005 after some larger rain events. Prior to clipping, the squares in grazed patches were protected from grazing.

During 2005, a variety of methods were used to assess the availabilities of N and P in the top 10 cm of soil. For N, we measured (1) total soil N, (2) inorganic N pool, (3) net N-mineralization, and (4) inorganic N-adsorption to ion-exchange resin-bags. For P, we measured (1) total soil P, (2) inorganic P, and (3) inorganic P-adsorption to ion-exchange resin-bags. At each site we collected five pairs of soil cores (2.8 cm diameter, 10 cm depth) using PVC tubes, four being arranged equidistantly (5 m) from a central one. One core from each pair served as the incubation sample for in situ net N mineralization, and was reinserted into the soil. The tube containing this core was closed with a lid at both the ends, and

contained holes above the soil surface to enable gas-exchange during incubation. The other core was used within 12 h to determine initial concentrations of inorganic N and P. To do this, NH_4^+ and NO_3^- were extracted from 10 g fresh soil using 50 ml of 0.2 M KCl, and PO_4^{2-} was extracted from 5 g fresh soil using 50 ml Bray-2 solution. KCl extracts were acidified with 5% H_2SO_4 for conservation until analysis. Concentrations of NO_3^-, NH_4^+ and PO_4^{2-} in the extracts were measured colorimetrically using a continuous flow injection analyzer (FIAStar, Foss Tecator, Höganäs, Sweden). In situ incubations for net N mineralization measurements were done for a 33 day interval in July 2005 and for a 19 day interval in November 2005, both at the transition from the wet to the dry season. Net N mineralization was calculated as the difference between extractable inorganic N at the start and at the end of the incubation interval. Additionally, total C and N were measured in the non-incubated soil cores using a dry combustion analyzer (CN-2000, LECO Corp., St. Joseph, Minnesota, USA), and total P was measured after Kjeldahl digestion as described for vegetation samples. Finally, we used ion-exchange resin bags (Dowex 1 [1X8-100] for anions and Dowex 50W [50X8100] for cations; Fluka, CH) to obtain an additional index of relative inorganic N and P availability among sites. Resin bags were prepared as described by Güsewell (2002): 1.00 ± 0.01 g of Dowex-1 and 0.76 ± 0.01 g of Dowex 50W were weighed into bags (3 cm × 4 cm) of nylon mesh (60 μm width, Sefar AG, Heiden, CH). Resins were conditioned by overnight immersion in a saturated KCl solution and 30 s rinsing with deionized water. At each site, five bags were placed carefully at 5 cm depth in 45° slant incisions made with a knife, after which the slides were closed. After 75 days, resin bags were collected from the field, gently rinsed with de-ionized water, and dried until extraction. Resin bags were extracted by shaking each bag for 90 min with 50 ml of 0.5 N HCl. The extraction solution was then analyzed colorimetrically for PO_4^{2-}, NO_3^- and NH_4^+ as described above.

Additionally, total pools of C, N, and P, and inorganic pools of N and P were determined along soil profiles in five savanna vegetation types (PD, PM, TG_M, TG_S, GP). At each site five soil cores to 70 cm depth were taken with a soil corer and split into five segments (0–10, 10–20, 20–30, 30–50, and 50–70 cm). For each depth, the five segments were pooled and analyzed using the methods described above. Soil bulk density was determined by digging a pit and extracting two large soil cores (4.2 cm diameter) per depth segment that were then dried to constant weight.

Input and Output Fluxes of Nutrient Balances

We measured wet atmospheric deposition of N and P in rain samples (n = 15) collected at regular intervals from October 2005 until November 2006. These were conserved by adding 0.5% H_2SO_4 and analyzed colorimetrically for PO_4^{2-}, NO_3^- and NH_4^+ as described above. Because of the small sample, however, we based our subsequent estimate of annual atmospheric deposition on published data for East Africa (2.5–5 kg N ha^{-1} y^{-1}; Augustine 2003; Galloway and others 2004, and 0.3 kg P ha^{-1} y^{-1}; Tamatamah and others 2005).

Symbiotic N_2-fixation was estimated for *Acacia* trees as well as legume herbs using measured data on biomass production, tissue N concentrations, and literature data for the proportion of N derived from the atmosphere (Ndfa). In August 2006, after the long wet season, we sampled the total biomass of herbaceous legumes and foliage of resprouting leguminous shrubs (mainly *Dichrostachys cinerea*) at each site from eight randomly placed frames of 1×1 m^2. Samples were dried, ground, and analyzed for N concentration using a dry combustion analyzer (CN-2000, LECO Corp., St. Joseph, Minnesota, USA). We assumed that the biomass harvested after the long wet season represented net annual production, because for the majority of the sites average time since the last fire was approximately 12 months. For *Acacia* woodlands we measured diameters of all *Acacia* trees at 20 cm height of 15×15 m^2 centered on the sites of soil sampling, and used the allometric equation from Cochard (2004) to estimate foliage mass after the long wet season, which was then used as an estimate for annual production. N concentration of *A. zanzibarica* leaves was determined from pooled leaf samples collected from two sites at the end of the wet season 2005; these had a mean value of 24.5 ± 0.5 mg N g^{-1}. For Ndfa of herbaceous legumes we used a range of published values from a mean of 80% observed in moist savanna species (Sanginga and others 1996) to the maximum observed value of 100% (for example, Sprent and others 1996). For woody legumes we used a range from $55 \pm 15\%$ (Cramer and others 2007). These Ndfa values corresponded well with our own estimates for the Saadani area (94 and 58% for legume herbs and *A. zanzibarica* trees, respectively) based on a few samples (Appendix B in Supplemental material).

Nutrient inputs in the dung of wild ungulates were estimated in three savanna types in the former Saadani game reserve by removing existing

dung from 100 m^2 plots and then collecting any dung dropped during the following approximately 45 days (5–14 January to 22–25 February 2007). The fresh dung was collected every 2 weeks, and numbers of pellets for each herbivore species were recorded (S. Halsdorf and C. Rohrer, unpublished data). Inputs of N and P were calculated using the average dry weight of fresh dung pellets per species, and the average N and P concentrations in fresh dung of almost all occurring herbivore species (buffalo, giraffe, kongoni, reedbuck, warthog, waterbuck, wildebeest) as measured after Kjeldahl digestion (S. Halsdorf and C. Rohrer, unpublished data). Dung concentrations of other herbivores were estimated using data for species with similar bodyweights and diet. Net deposition of N in urine was calculated from the measured dung input. In the absence of data for wild herbivores, we used values from Scholefield and others (1991), who reported that cows on a low nitrogen diet excreted 45 % of the N they ingested in the form of urine. We also assumed that 3–25% of urea (or 85% of urinary N) was lost through ammonia volatilization, as reported by Ruess and McNaughton (1988) for wildlife in the Serengeti. Due to the very low proportion of P excreted in urine (Morse and others 1992) this input was regarded as negligible.

Nutrient losses through fire were determined in burning experiments conducted in the early dry season 2006 in three vegetation types—tallgrass savanna, *Acacia* woodland, and forest gap. The experimental design was fully factorial with respect to the origin of biomass and burning location, and each vegetation type was replicated three times. Total aboveground herbaceous biomass was collected at around midday by clipping two adjacent 50 × 50 cm^2 squares to approximately 3 cm height. After weighing the biomass samples, one of the samples was dried and later used to determine the nutrient content of unburnt vegetation. The second sample was stacked in a metal frame with a 50 × 50 cm^2 base, designed to hold the plant material as in a natural stand, and ignited using a 50 cm long torch placed upwind for 30 s. When the fire was over, the residue was collected and separated into unburned green biomass, unburned dead biomass and ash. Oven-dried samples were milled, digested (Kjeldahl method), and analyzed for N and P concentrations. The relative total nutrient loss was calculated from the nutrient content in pre-burning reference samples and post-burning residues. Weather conditions during the burning of the samples (wind speed, temperature, and relative humidity) were recorded as co-variables. These did not vary significantly between days, and there was also no effect of location of the experimental burnings within different vegetation types on relative nutrient losses (data not shown). The total losses caused by a single early dry season fire event in a particular vegetation type were estimated based on the measured nutrient content in aboveground biomass and the experimentally measured relative total nutrient loss. Permanent losses from the ecosystem are more likely for those nutrients transferred to the atmosphere in gaseous or non-particulate form (Raison and others 1985). Therefore, net fire losses were estimated from total losses accounting for the proportion of nutrients transferred in non-particulate form (97% for N, 20% for P; Laclau and others 2002).

Statistics

Statistical analysis was performed with JMP 6.0.3 (SAS Institute, Cary, USA). We used analysis of variance (type III SSQ, factors ''vegetation type'' and ''gradient'') to explore trends along the vegetation gradients, and made multiple comparisons between factor levels using the Tukey–Kramer HSD test ($P < 0.05$). If necessary, data were log-transformed prior to analysis to meet model assumptions. Data from tallgrass sites in the former game reserve (TG$_S$) were compared with data from nearby grazed patches (GP), and with data from tallgrass sites in the former ranch (TG$_M$) using Student's t test assuming unequal variances.

RESULTS

Vegetation

Aboveground herbaceous biomass—and the associated pools of N and P—was highest in the former paddocks (Table 1). There were no significant differences between the other vegetation types along the gradient, although N pools in aboveground biomass tended to be higher in tallgrass savanna, whereas P pools tended to be high in both tallgrass savanna and paddock margins. The N pool in aboveground vegetation was significantly lower in grazed patches than in nearby ungrazed tallgrass sites (Table 1). The productivity of herbaceous vegetation was highest in paddock margins and tallgrass savanna (Table 1). In tallgrass savanna, the aboveground biomass contained 1.7% of the total N pool and 1.8% of the P pool (that is, the total biomass plus top 30 cm of soil), and the corresponding values in paddock margins and grazed patches were 1.4 and 0.7% for N and 2.8 and 0.9% for P, respectively. On average more than 50% of

Table 1. Nutrient Pools in Topsoil and Aboveground Herbaceous Vegetation of Various Savanna Types

	Paddock gradients					Saadani sites	
	PD	PM	HS	AW	TG$_M$	TG$_S$	GP
Topsoil (10 cm)							
Total C (kg m^{-2})	3.79 ± 0.82^a	0.84 ± 0.10^b	1.64 ± 0.54^{ab}	1.66 ± 0.16^{ab}	0.72 ± 0.15^b	0.89 ± 0.04	1.16 ± 0.25
Total N (g m^{-2})	367 ± 78^a	73 ± 9^b	116 ± 33^b	124 ± 9^b	55 ± 10^b	66 ± 5	89 ± 18
Total P (g m^{-2})	98 ± 29^a	7.8 ± 1.5^b	8.6 ± 1.9^b	9.2 ± 0.9^b	5.3 ± 0.9^b	7.3 ± 0.1	11.0 ± 2.7
Extractable N Jul '05 (g m^{-2})	5.9 ± 2.4^a	0.29 ± 0.08^{bc}	0.19 ± 0.06^c	0.41 ± 0.08^b	0.21 ± 0.04^{bc}	0.30 ± 0.07	0.44 ± 0.12
Extractable N Nov '05 (g m^{-2})	6.1 ± 3.4^a	0.32 ± 0.04^b	0.63 ± 0.20^{ab}	0.59 ± 0.05^{ab}	0.28 ± 0.09^b	0.13 ± 0.04	0.30 ± 0.15
Extractable P Jul '05 (g m^{-2})	51 ± 27^a	0.73 ± 0.15^b	0.19 ± 0.01^b	0.28 ± 0.05^b	0.35 ± 0.11^b	0.32 ± 0.08	0.82 ± 0.18‡
Extractable P Nov '05 (g m^{-2})	63 ± 22^a	0.81 ± 0.27^b	0.21 ± 0.03^b	0.25 ± 0.05^b	0.34 ± 0.08^b	0.21 ± 0.05	0.57 ± 0.12‡
Aboveground herbaceous biomass							
Biomass Jul '05 (kg m^{-2})	1.44 ± 0.14^a	0.56 ± 0.07^b	0.45 ± 0.10^b	0.35 ± 0.20^b	0.98 ± 0.19^{ab}	0.87 ± 0.09	0.16 ± 0.06*
Proportion of dead biomass (%)	55 ± 2^a	57 ± 8^a	61 ± 2^a	48 ± 4^a	46 ± 10^a	60 ± 4	47 ± 5*
[N] live biomass (mg g^{-1})	14.0 ± 0.82^a	5.4 ± 0.34^c	5.3 ± 0.02^c	8.0 ± 0.41^b	3.9 ± 0.26^d	3.8 ± 0.64	10.1 ± 2.0*
[N] dead biomass (mg g^{-1})	12.7 ± 1.0^a	3.2 ± 0.18^{cd}	3.5 ± 0.34^c	5.0 ± 0.38^b	2.5 ± 0.01^d	2.5 ± 0.09	5.3 ± 1.0*
[P] live biomass (mg g^{-1})	2.26 ± 0.35^a	1.15 ± 0.38^{ab}	0.40 ± 0.03^b	0.46 ± 0.03^b	0.44 ± 0.07^b	0.45 ± 0.06	1.20 ± 0.29*
[P] dead biomass (mg g^{-1})	2.13 ± 0.23^a	0.38 ± 0.11^b	0.21 ± 0.03^b	0.23 ± 0.03^b	0.19 ± 0.02^b	0.20 ± 0.02	0.53 ± 0.13*
Total N Jul '05 (g m^{-2})	19 ± 1^a	2.3 ± 0.2^b	1.9 ± 0.5^b	2.2 ± 1.1^b	3.2 ± 0.8^b	2.5 ± 0.2	1.1 ± 0.2*
Total P Jul '05 (g m^{-2})	3.1 ± 0.2^a	0.38 ± 0.11^b	0.13 ± 0.04^b	0.13 ± 0.07^b	0.35 ± 0.13^b	0.26 ± 0.06	0.13 ± 0.05
Production Jul-Dec '05 (g m^{-2})	291 ± 102^{a,1}	95 ± 13^{b,1}	65 ± 26^{b,2}	59 ± 13^b	165 ± 12^{ab}	225 ± 80	132 ± 9

Data are presented for three paddock gradients on former cattle ranch grounds, and at three grazed and ungrazed sites in the former Saadani game reserve. Values are means per vegetation type.
Precipitation during the period of biomass production measurements was 176 mm at paddock gradient sites and 241 mm at Saadani sites.
PD = former paddocks, PM = paddock margins, HS = Heteropogon savanna, AW = Acacia woodland, TG$_M$ = tallgrass savanna of the former Mkwaja ranch, TG$_S$ = tallgrass savanna in the former Saadani game reserve, GP = grazed patches.
[1]*One of three sites burned during the measurement period (see also Appendix A in Supplementary material).*
[2]*Two of three sites burned during the measurement period (see also Appendix A in Supplementary material)*
Values for paddock gradients not sharing the same letter are significantly different (Tukey-HSD, P < 0.05).
*[*],[‡]*Significant differences between TG$_S$ and GP sites (t test) at P < 0.05 and P < 0.10, respectively. There were no significant differences between TG$_M$ and TG$_S$ sites (t test, P < 0.10).*
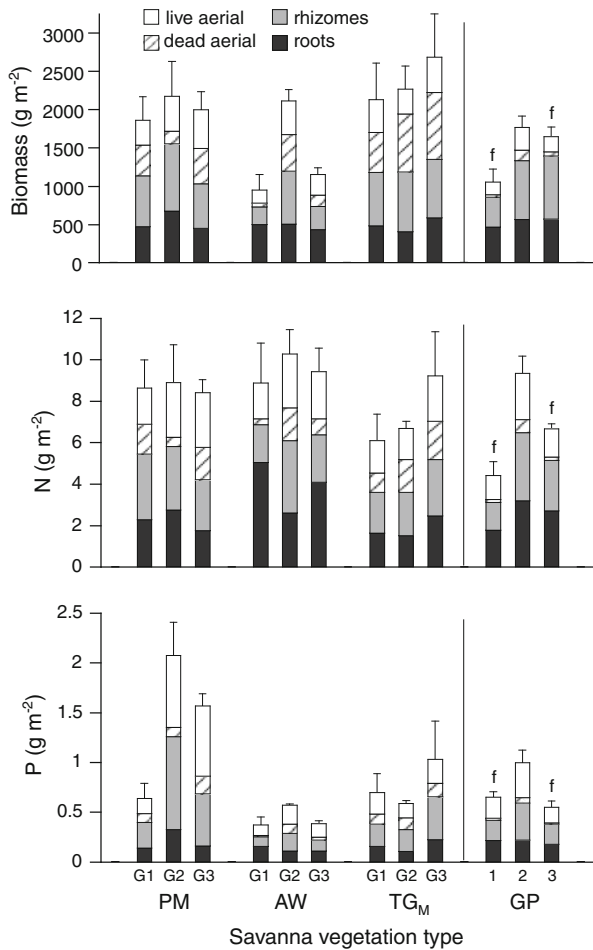
Figure 3. Total herbaceous biomass and biomass nutrient pools in four selected savanna types in January 2007: paddock margins (PM), *Acacia* woodland (AW), and tallgrass savanna (TG$_M$) were located along paddock gradients, and three intensively grazed sites (GP) were located in the former Saadani game reserve. Biomass and nutrient pools are shown for live and dead aboveground biomass, as well as for rhizomes and roots. Sites marked with an "*f*" burned 1–2 months before the measurements. *Error bars* indicate standard errors of total biomass (n = 4).

the nutrient pools in vegetation was in belowground structures (Figure 3).

The concentrations of N and P in aboveground vegetation were highest in the former paddocks, but also relatively high in the grazed patches (Table 1). In the former paddocks, N and P concentrations remained high in the dead biomass, indicating that less than 10% of these nutrients was withdrawn before senescence. In the other sites N and P concentrations were considerably lower in dead than in living biomass, between 34 and 48% for N and 48 and 67% for P was withdrawn.

The N:P ratios in live aboveground vegetation were consistent with our expectations (see
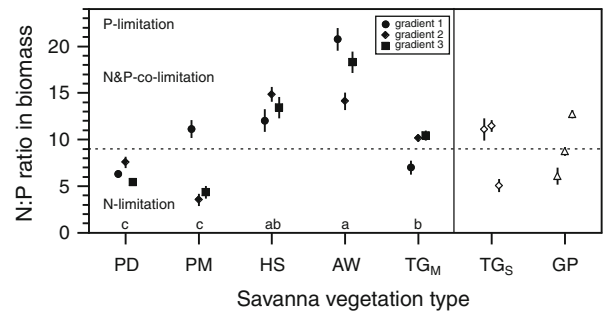

Figure 4. Relative availabilities of N and P along paddock gradients in a former cattle ranch and reference sites in a former game reserve as measured by the N:P ratio in live aboveground herbaceous biomass in July 2005. *PD* = former paddocks, *PM* = paddock margins, *HS* = *Heteropogon* savanna, *AW* = *Acacia* woodland, *TG$_M$* = tallgrass savanna of the former Mkwaja ranch, *TG$_S$* = tallgrass savanna in the former Saadani game reserve, *GP* = grazed patches. *Open symbols* from left to right are for TG$_S$ and GP sites 1, 2, and 3. Data show means per site (n = 4, ±SE). The *dashed line* represents the boundary between N-limitation and NP-co-limitation based on a study by Cech and others (2008) The available data are not sufficient to distinguish a critical value between NP-co-limitation and P-limitation, or to determine whether there is such a value at all (Cech and others 2008).

Figure 2B) of high availability of P relative to N in former paddocks and margins, and high N relative to P in *Acacia* woodlands (Figure 4). There was, however, considerable variation in N:P ratios among sites of the same vegetation type (Figure 4). For instance, in *Acacia* woodlands, the availability of N relative to P was higher on gradients 1 and 3, which had higher densities of *Acacia* trees than on gradient 2 (Figure 4).

Soil Nutrient Pools

Pools of carbon, nitrogen, and phosphorus were higher in the former paddocks than in paddock margins, *Heteropogon* savanna and *Acacia* woodlands, and were lowest in tallgrass savanna (Table 1, Appendix A in Supplemental material). In most cases, the only significant differences were between the former paddocks and the other sites, though this may partly have been due to low statistical power. The enrichment in total soil N and P in the former paddocks was measurable even in the deepest samples (70 cm), and was more pronounced for P than for N (Figure 5).

Pools of inorganic N along the paddock gradients in July 2005 corresponded to the pattern expected from Figure 2B, although in most cases only the differences between former paddocks and the other vegetation types were significant (Table 1,
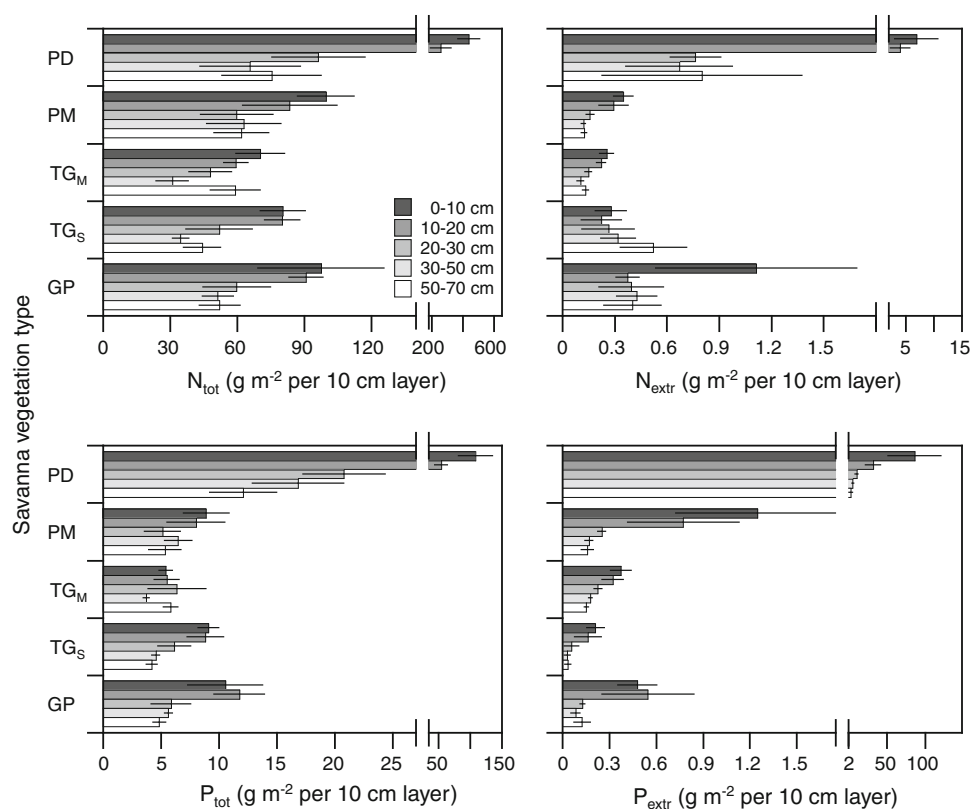
Figure 5. Pools of total N, total P, and extractable inorganic N and P, along soil profiles in five selected savanna types: former paddocks (PD), paddock margins (PM), and tallgrass savanna (TG$_M$) were located along paddock gradients; tallgrass savanna (TG$_S$) and intensively grazed patches (GP) were located in the former Saadani game reserve. *Error bars* indicate standard errors (n = 3).

Appendix A in Supplemental material). The mean inorganic N pools in November 2005 were higher than those in July, particularly in *Heteropogon* savanna. The enrichment in inorganic N-pools in the former paddocks relative to the other sites was most pronounced in the top 20 cm and declined with increasing depth (Figure 5).

Pools of inorganic P along paddock gradients were rather similar in July and November, and matched the expected pattern (Figure 2B); again, only former paddock sites were significantly different from the other sites (Table 1). P-enrichment in former paddocks was evident down to 70 cm soil depth, and was more pronounced relative to the enrichment observed for extractable N (Figure 5). Elevated levels of extractable P in paddock margins and grazed patches were confined to the top 20 cm (Figure 5). Grazed patches tended to have higher pools of extractable phosphorus than nearby tallgrass sites (Table 1).

Soil Nutrient Turnover Rates

Rates of N mineralization varied widely, and some were even negative (Figure 6A, B). The trend in net N mineralization rates along paddock gradients was similar to that observed for inorganic N pools (Figure 5; Table 1), with the highest values in the former paddocks (compare Figures 6, 2B). N min-

eralization tended to be higher in *Acacia* woodlands than in adjacent vegetation types, but only during the first incubation period (Figure 6). It also tended to be higher in grazed areas than in nearby tallgrass sites, though the differences were not significant (Figure 6, $P > 0.05$).

Rates of inorganic N release as measured by adsorption to resin bags were generally consistent with the patterns in N mineralization rates found in the first incubation period (compare Figure 6A, C), with values in the former paddocks being significantly higher than in the other vegetation types (Figure 6C). N mineralization also tended to be faster in grazed patches than in nearby tallgrass sites, but this difference was not significant (Figure 6, $P = 0.08$).

Adsorption of inorganic P to resin bags declined steadily along the paddock gradients (Figure 6D). Grazed patches showed on average higher P adsorption than nearby tallgrass sites, but this was not statistically significant ($P = 0.28$).

Nutrient Input and Output Fluxes and Balances

The mean N concentration in rain samples was 0.67 ± 0.12 mg l^{-1} (0.41 ± 0.12 NO$_3$-N and 0.26 ± 0.05 NH$_4$-N), whereas that of P was 34 ± 10 μg l^{-1}
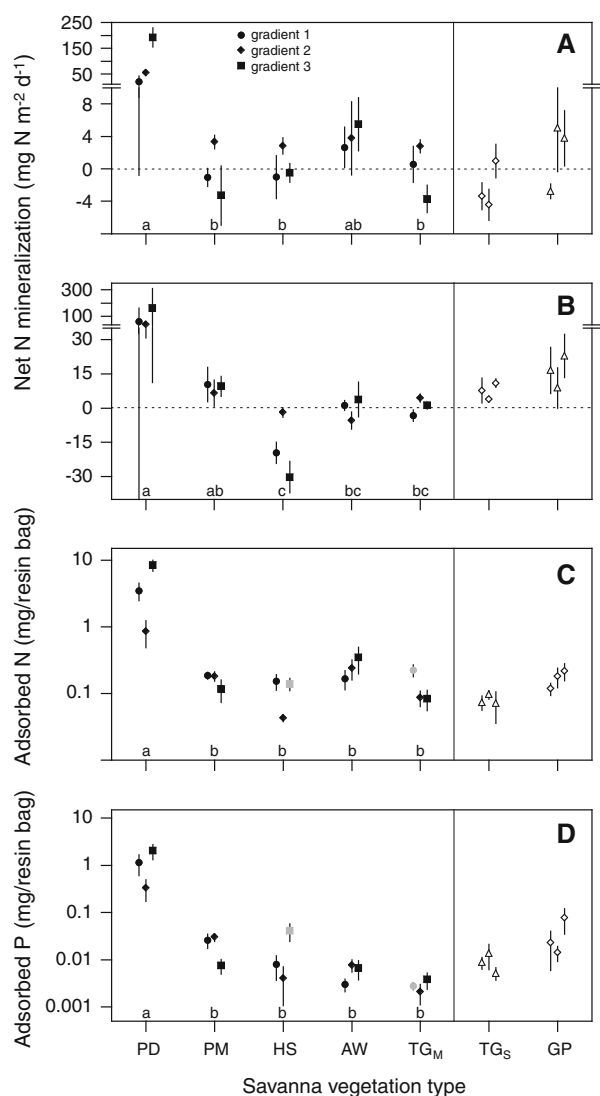
Figure 6. Net N mineralization rates and adsorption rates of N and P on resin along three paddock gradients on former cattle ranch grounds, and at three tallgrass savanna and three grazed sites in the former Saadani game reserve. Net N mineralization rates were measured in situ for a 33 day incubation period in July/August 2005 (**A**), and for a 19 day incubation period in November/December 2005 (**B**). Adsorption rates of inorganic N (**C**) and inorganic P (**D**) to ion-exchange resins were determined between September and November 2005. *PD* = former paddocks, *PM* = paddock margins, *HS* = *Heteropogon* savanna, *AW* = *Acacia* woodland, TG_M = tallgrass savanna of the former Mkwaja ranch, TG_S = tallgrass savanna in the former Saadani game reserve, *GP* = grazed patches. *Open symbols* from left to right are for TG_S and GP sites 1, 2, and 3. *Gray symbols* indicate that the site burned while resin bags were in the soil. *Error bars* indicate standard errors (n = 5). Savanna types along paddock gradients not sharing the *same letter* are significantly different (n = 3, Tukey-HSD, $P < 0.05$). *Note:* in panels (**A**) and (**B**) the *y*-axis breaks at 10 and 35, respectively, and continues with a different scale. In panels (**C**) and (**D**) data are shown on a log scale.

(PO_4-P). From these data and average long-term precipitation of 1040 mm y^{-1}, we calculated atmospheric deposition rates at 7.0 kg N ha^{-1} y^{-1} and 0.35 kg P ha^{-1} y^{-1}. Combining these values with the published data for East Africa, we obtained a range of estimates for wet atmospheric deposition of 2.5–7.0 kg N ha^{-1} y^{-1} and 0.30–0.35 kg P ha^{-1} y^{-1}.

Annual inputs of N and P in dung were significantly higher in heavily grazed areas than in nearby tallgrass savanna (Table 2). Nutrient inputs in *Acacia* woodlands were intermediate among those in the other vegetation types.

Tree densities of *A. zanzibarica* in *Acacia* woodlands were 2620, 840, and 2440 per ha for the sites on gradients 1, 2, and 3, respectively. The N fixation in *Acacia* woodlands was estimated to range between 3 and 12 kg N ha^{-1} y^{-1} according to the density of the stand (Table 3). The contribution from N_2-fixation by herbaceous legumes was very low in all savanna types, and did not exceed 0.50 kg N ha^{-1} y^{-1} (Table 3).

On average, 71% of N in the aboveground biomass was lost through burning whereas only 27% of P was lost (Table 4). These percentages for N and P were significantly different ($P < 0.05$). The percentage nutrient losses were similar for the three savanna types (Table 4). The proportion of dead material in the biomass was lowest in the vegetation type most prone to fire, tallgrass savanna, and highest in forest gaps, which are largely protected from fire (Table 4; compare Cech and others 2008). Relative losses of N tended to increase with the proportion of dead biomass, but losses of P were similar in all vegetation types (Table 4). The net losses caused by a single early dry season fire event were estimated at 129 kg N ha^{-1} and 1.7 kg P ha^{-1} in the former paddocks, and 13–22 kg N ha^{-1} and 0.1–0.2 kg P ha^{-1} in the other vegetation types (data not shown).

The estimated average annual N balances were negative in all vegetation types except *Acacia* woodlands, which tended to have a positive net N balance (Figure 7, Appendix D in Supplemental material). The estimated annual P balances tended to be negative in former paddocks and in grazed areas, and positive in the other vegetation types.

DISCUSSION

Soil Nutrient Pools and Turnover Rates

Apart from in the former paddocks, the soils of the moist savanna in the Saadani region were rather nutrient poor when compared to most other African

Table 2. Nitrogen and Phosphorus Input Rates from Herbivore Dung in various Savanna Types

Habitat	n	N (kg ha^{-1} y^{-1})	P (kg ha^{-1} y^{-1})	N:P
Tallgrass savanna	5	0.40 ± 0.19[b]	0.07 ± 0.04[b]	4.7 ± 0.2
Grazed patches	6	6.36 ± 1.81[a]	0.99 ± 0.32[a]	6.8 ± 0.6
Acacia woodland	4	1.96 ± 1.03[ab]	0.33 ± 0.15[ab]	5.3 ± 0.6
Medium height savanna	5	3.57 ± 1.42[ab]	0.67 ± 0.28[ab]	5.3 ± 0.6

Data are shown for four vegetation types in the area of the former Saadani game reserve.
Calculations are based on unpublished data from S. Halsdorf and C. Rohrer.
Values not sharing the same letter indicate significant differences among vegetation types (Tukey-HSD, P < 0.05).

Table 3. N Content and Estimated N-Fixation in Herbaceous and Woody Legumes in Various Savanna Types

	Paddock gradients					Saadani sites	
	PD	PM	HS	AW	TG$_M$	TG$_S$	GP
Herbaceous legumes							
N in total biomass of herbaceous legumes (kg ha^{-1})							
Gradient/site 1	0	0.31	0.20	0.13	0.47	0.50	0.40
Gradient/site 2	0	0	0.44	0.03	0.16	0.25	0.09
Gradient/site 3	0	0.32	0.03	0	0.32	0.32	0.31
Estimated N fixed (kg ha^{-1})							
Min–max	0–0	0–0.32	0.02–0.44	0–0.13	0.13–0.47	0.20–0.50	0.07–0.40
Mean (n = 3)	0	0.19 ± 0.11	0.20 ± 0.12	0.05 ± 0.03	0.29 ± 0.16	0.32 ± 0.19	0.24 ± 0.14
Woody legumes							
N in foliage of woody legumes (kg ha^{-1})							
Gradient/site 1	0	0	0.17	17.2	0	0	0
Gradient/site 2	0	1.11	0	6.9	0	0	0.03
Gradient/site 3	0	0	1.14	16.3	0	0	0.04
Estimated N fixed (kg ha^{-1})							
Min–max	0–0	0–0.8	0–0.8	2.8–12.0	0–0	0–0	0–0
Mean (n = 3)	0	0.2 ± 0.1	0.2 ± 0.1	7.4 ± 4.3	0	0	0

For herbaceous legumes N content was measured from total biomass.
For woody legumes N content in foliage of small shrubs was measured, for Acacia trees N concentration in foliage was measured and foliage biomass calculated from allometric equations from Cochard (2004).
Symbiotic N$_2$-fixation was estimated using ranges for the proportion of N derived from the atmosphere (Ndfa) of 80–100% for herbaceous and 40–70% for woody legumes (for more details see the ''Methods''). Minimum estimated N$_2$-fixation of herbaceous legumes was calculated as 80% of the lowest measured value of N in total legume biomass among the three sites, and the maximum as 100% of the highest measured value. Mean estimated N$_2$-fixation in herbaceous legumes is the average of three sites, using the measured amount of N in total legume biomass at each site and 90% Ndfa. For woody legumes min/max and means were calculated as for herbaceous legumes, but using the amount of N in foliage and Ndfa values of 40/70 and 55% respectively.
PD = former paddocks, PM = paddock margins, HS = Heteropogon savanna, AW = Acacia woodland, TG$_M$ = tallgrass savanna of the former Mkwaja ranch, TG$_S$ = tallgrass savanna in the former Saadani game reserve, GP = grazed patches; (same sites as in Table 1).

**Table 4.** Nitrogen and Phosphorus Losses through Fire from Herbaceous Vegetation

	Acacia woodland	Tallgrass savanna	Forest gaps
Characteristics of biomass prior to burning			
Dry weight (g m^{-2})	1025 ± 77[a]	990 ± 30[a]	1120 ± 90[a]
% Dead	72 ± 2[b]	59 ± 2[c]	84 ± 1[a]
Water content (%)	38 ± 2[a]	33 ± 1[b]	24 ± 1[c]
Percentage nutrient loss through burning			
Nitrogen (%)	71 ± 2[a]	67 ± 3[a]	75 ± 3[a]
Phosphorus (%)	28 ± 4[a]	25 ± 3[a]	28 ± 3[a]

Nutrient losses were measured from combustion experiments, and are given in percent of total content in pre-burned aboveground herbaceous biomass.
Data per site are means of nine replicate combustions done in the early dry season in August 2006 (±SE).
Values not sharing the same letter indicate significant differences among vegetation types (Tukey-HSD, P < 0.05).
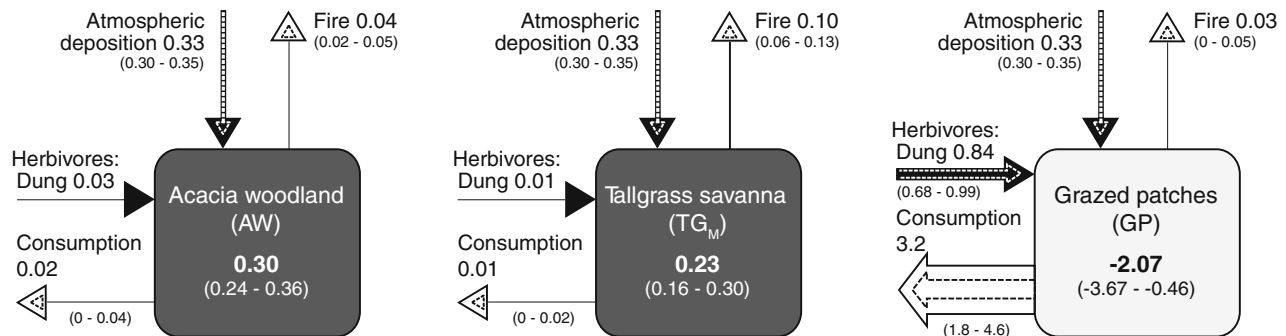
Nitrogen
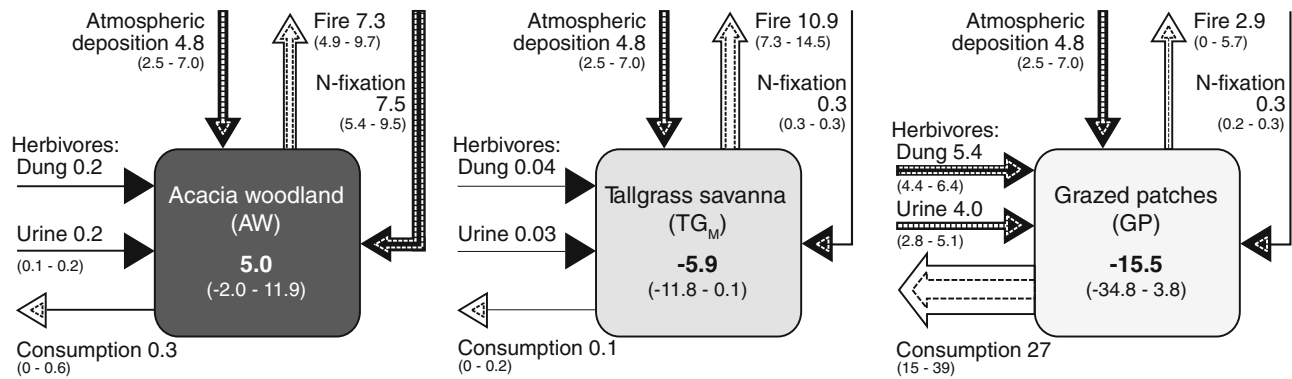
Phosphorus

Figure 7. Estimated nitrogen and phosphorus budgets for two selected vegetation types along paddock gradients in the former Mkwaja Ranch area, and of grazed patches in the former Saadani game reserve. *Values* indicate average fluxes based on our own measurements and literature data; those in *brackets* indicate average minimum and average maximum fluxes from three replicate sites. All fluxes are given in kg ha^{-1} y^{-1}. Inner and outer *arrows* show the lower and upper estimates of a flux. *Arrow* width represents the relative size of the input/output when compared to other fluxes. Values in the *boxes* show the average net fluxes (minimum and maximum average net fluxes are in brackets). As a rough assessment for the average N-fixation which is required for an average neutral N balance, one can subtract the mean values in the *boxes* from the mean assessed value for N-fixation (yielding 2.5, 6.2, and 15.8 kg in kg ha^{-1} y^{-1} for Acacia woodland, Tallgrass savanna, and Grazed patches, respectively). See ''Methods'' and Appendix D in Supplementary material for details on calculations.

savannas that have been studied. Thus, total and extractable P concentrations (0.04–0.08 g kg^{-1}) were much lower than those in the semi-arid savannas of the Serengeti (0.6–6 g kg^{-1}) or in Kenya (0.2 g kg^{-1}), and in a littoral savanna in Congo (0.2–0.3 g kg^{-1}) (Ruess and McNaughton 1987; Laclau 2003; Augustine 2004). Total and inorganic N concentrations (0.4–0.8 g N_{tot} kg^{-1} and 1–3 mg N_{inorg} kg^{-1}) were also considerably lower than those in the Serengeti (1–4 g N_{tot} kg^{-1} and 5–13 mg N_{inorg} kg^{-1}) (Ruess and McNaughton 1987), but in the same range as in humid savannas in West Africa (0.3–0.5 g N_{tot} kg^{-1} and ≤ 2 mg N_{inorg} kg^{-1}) (de Rham 1973; Abbadie 1990; Laclau 2003).

Trends in inorganic pools of N and P along the paddock gradients were generally consistent with

our expectations (Figure 2B), and reflected the relative availabilities of these nutrients as indicated by N:P ratios in living plant tissue and by differences in nutrient resorption from dying leaves (compare Table 1; Figure 4). The fact that the concentrations of N within and in the margins of the former paddocks were less extreme than those of P probably reflects the loss of N from dung and urine through volatilization (Augustine 2003). This is consistent with the significantly higher δ^{15}N values in soils of former paddocks when compared to surrounding sites reported by Treydte and others (2006a). The difference between N and P could also reflect more leaching of inorganic N than of the less mobile P. The relatively high N and P concentrations in deeper soil layers in the former paddocks

suggest that significant amounts of both nutrients were lost by leaching (Figure 5). Total and extractable nutrient pools in former paddocks were comparable to those from a chronosequence of abandoned paddocks (bomas) 12–24 years old in a semi-arid savanna in Kenya (Augustine 2003). In that study, soil N pools in paddocks were found to decrease more rapidly than soil P pools, which is consistent with our data measured 6 years after abandonment of the ranch (compare Table 1; Figure 5). However, our data show that the enrichment of P relative to N was not confined to the small area of the former paddocks (0.2% of the total ranch area), but extended into the surrounding vegetation (PD + PM comprise 3.3% of the total area). In Sahelian rangelands, also, P availability was increased at distances of up to 5 km from watering points (Turner 1998).

As expected (Figure 2B), rates of soil P release (adsorption to resins) declined gradually with distance from the former paddocks. However, the same pattern was not observed for the measures of N turnover (N mineralization and adsorption to resins), except that these were highest in the former paddocks (Figure 6). Contrary to what has been found in other areas invaded by *Acacia* species (Stock and others 1995; Yelenik and others 2004), nitrogen turnover was not significantly higher in *Acacia* woodlands than in adjacent tallgrass savanna. However, the data for soil pools and N:P ratios in plants indicate that N availability was higher in the *Acacia* woodlands.

Soil inorganic P pools tended ($P < 0.10$) to be higher in the patches grazed by wild herbivores than in nearby tallgrass savanna (Table 1; Figure 5, Appendix A in Supplemental material). Also, the average N and P concentrations in living plants were relatively high in the grazed patches (Table 1). It is not possible to determine whether the animals selected the most nutrient-rich areas, or whether their activities enhanced soil P availability in the same way as cattle did in paddocks. To judge from the very large variation in total and inorganic N and P pools in grazed patches, however, it seems unlikely that soil nutrient concentrations strongly influence food selection by wild herbivores (Figure 5). On the other hand, their activities of grazing and excretion may promote grass species that are tolerant of defoliation and relatively nutrient-rich, and these in turn may be preferred by herbivores (Cech 2008, and unpublished data).

We conclude that herbivores, fire, and invasion by *Acacia* trees all influence the relative availabilities of nitrogen and phosphorus, much as predicted in Figure 2B. However, except for the highly enriched former paddocks, availabilities of nutrients and mineralization rates do not fully explain patterns in biomass and productivity, because relatively high productivity values were observed in tallgrass savanna, which had the lowest levels of nutrient availability (Table 1). Abbadie and others (1992), working at Lamto in West Africa, concluded that grasses derived most of their nitrogen by reabsorbtion from senescing roots rather than by uptake of N released by mineralization. It may be that reabsorbtion is also an important source for nutrients in our tallgrass savanna.

Nutrient Input and Output Fluxes and Balances

We assessed annual N and P balances for various savanna types in the Saadani region by scaling up results of our measurements and experiments, making use of published data where necessary. Although rough, these estimates are useful for determining the relative importance of the different factors that influence N and P availabilities, and assessing the implications of different management strategies (for example, burning). In addition, constructing balances helps identify where there are important gaps in our knowledge that require further research.

Our estimates of wet atmospheric deposition of N and P based on literature data from East Africa and our own measurements were in line with values reported for other savanna ecosystems (1.3–6.4 kg N and 0.3–0.5 kg P ha^{-1} y^{-1}) (Montes and San Jose 1989; Chacon and others 1991; Sanhueza and Crutzen 1998; Laclau and others 2005; Bustamante and others 2006). Dry deposition is likely to be minimal in our study area because the prevailing winds come from the Indian Ocean; this was also found for a coastal savanna in Congo (Laclau and others 2005).

We estimated that N$_2$ fixed in *Acacia* woodlands ranges between 3 and 12 kg N ha^{-1} y^{-1}, depending on the density of the trees (Table 3). This estimate is based on a range for the proportions of N derived from the atmosphere (Ndfa) of 40–70% from data for several African *Acacia* tree species and *Dichrostachys cinerea* (Cramer and others 2007), and takes only biomass production of the leaves into account. Despite methodological limitations, our estimate of 58% Ndfa for *Acacia zanzibarica* (see Appendix B in Supplemental material) lies in the middle of the published range. Furthermore, the upper limit of our N input rates in *Acacia zanzibarica* woodlands agrees with the reported value of about 12 kg N ha^{-1} y^{-1} for *Acacia pellita* plantations in Australia (Langkamp and others 1979).

Our estimate of Ndfa in legume herbs of our study area (^{15}N natural abundance method) of 94% fits well in the published range of 80–100%, but for methodological reasons may be less accurate (see Appendix B in Supplemental material). Despite these high Ndfa values, however, the N input from symbiotic N_2-fixation of herbaceous legumes was very low in all vegetation types (≤ 0.5 kg N ha^{-1} y^{-1}), and much lower than those reported (or assumed) for other savannas (for example, Sanhueza and Crutzen 1998; Laclau and others 2005). In a previous paper, we showed that the very low abundance of herbaceous legumes in our area is probably due to the competitive superiority of C_4 grasses (Cech and others 2010).

Animal excreta only affect nutrient balances substantially in heavily used areas such as grazed patches (Figure 7). Deposition of dung by bison and elk in Yellowstone National Park was estimated at 0–410 kg ha^{-1} y^{-1} (Frank and McNaughton 1992), but we are unaware of comparable data for wild herbivores in savanna. At 390 ± 140 kg ha^{-1} y^{-1}, the input of dung to grazed patches in our study area was at the upper end of this range. The P returned to grazed patches by wild herbivores (about 0.7–1.0 kg P ha^{-1} y^{-1}, Figure 7) was much lower than that returned by cattle in paddocks during the time of the ranch (estimated at 47 kg P ha^{-1} y^{-1}) or even in the areas surrounding the paddocks (2.3 kg P ha^{-1} y^{-1}) (see Appendix C in Supplemental material). However, because the normally abundant wildebeest were absent from our area during the study period (S. Halsdorf, personal communication), we may have underestimated the return of dung deposition to grazed patches.

Herbivores were scarce in most of the savanna types, and nutrient removal in offtake was probably negligible except in patches that were particularly favored by animals (Figure 7, Appendix D in Supplemental material). Such a heterogeneous pattern of offtake, which has also been demonstrated in semi-arid savanna (Van de Vijver and others 1999), probably develops because regrowth contains higher concentrations of nutrients and is therefore grazed repeatedly (Hobbs 1996). Even though nutrient concentrations were highest in vegetation of the former paddocks (Table 1), there were only very few signs of grazing (Cech, personal observation), probably due to the low density of wild herbivores on the area of the former cattle ranch (Treydte and others 2005). Measuring productivity of grazed patches by repeated clipping, as we did in this study, is likely to be less accurate than using the moveable cage method (Augustine and others 2003) because grazing may stimulate or reduce growth when compared to clipping. For grazed areas in the Serengeti, annual primary productivity measured with moveable cages was 2–14 ton ha^{-1} y^{-1} which compared to 1–6 ton ha^{-1} y^{-1} in permanent exclosures (McNaughton 1985). Although our results may underestimate the offtake of herbage, they do suggest that intensive grazing by wild herbivores may gradually reduce nutrient pools (Figure 7, Appendix D in Supplemental material).

The largest nutrient losses in the ungrazed savanna types were due to fire, especially in tallgrass savanna with a high aboveground biomass. Scaling up the results of our burning experiment, we estimate that a single fire in the dry season would cause a net loss of 13–22 kg N and 0.1–0.2 kg P ha^{-1}. The values for N are within the published range for savanna ecosystems (10–23 kg ha^{-1} for N), whereas those for P are somewhat lower (0.3–0.5 kg ha^{-1}; Villecourt and others 1980; Cook 1994; Kauffman and others 1994; Laclau and others 2002; Rossiter-Rachor and others 2008). However, the annual nutrient losses through fire may be considerably lower or higher, depending on the fire frequency (Figure 7, Appendix D in Supplemental material). For national parks such as Saadani, in which the vegetation is commonly burned in the early dry season to attract wildlife and prevent uncontrollable late-dry-season fires (Eriksen 2007), a typical frequency would be once or twice for every 3 years, which we applied for calculations in Figure 7.

The inputs and outputs shown in Figure 7 and Appendix D (Supplemental material) are not exhaustive and may omit some significant fluxes. For example, non-symbiotic biological N_2-fixation by cyanobacteria was found to be 3–9 kg N ha^{-1} y^{-1} in a Nigerian savanna (Isichei 1980), but less than 0.04 kg N ha^{-1} y^{-1} in Southern Africa (Aranibar and others 2003a), and 1–2 kg N ha^{-1} y^{-1} in Venezuela (Sanhueza and Crutzen 1998). Furthermore, N_2-fixation by rhizosphere associations was estimated at 1–8 kg N ha^{-1} y^{-1} in Venezuela (Sanhueza and Crutzen 1998) and 10 kg N ha^{-1} y^{-1} in the Ivory Coast (Balandreau 1976), but could not be demonstrated in a study in Southern African savannas (Bate and Gunton 1982). Hence, N input from non-symbiotic fixation could be of a magnitude similar to that from symbiotic N_2-fixation in dense Acacia woodlands, but whether this is the case in the Saadani region, and how it varies among savanna types, are unknown.

Nitrogen can be lost from ecosystems through denitrification, but this flux is probably negligible from well-drained savanna soils (Chacon and others 1991; Le Roux and Mordelet 1995; Sanhueza

and Crutzen 1998; Serca and others 1998). Data on leaching losses for humid savannas are scarce and vary widely, whereas these are likely to be minimal in semi-arid savanna (Bate and Gunton 1982; Dougill and others 1998), measured losses were 5.6 kg N ha^{-1} y^{-1} and 0.58 kg P ha^{-1} y^{-1} in Lamto savanna (Villecourt and Roose 1978), and 3.0 kg N ha^{-1} y^{-1} and 0.1 kg P ha^{-1} y^{-1} in a savanna in Congo (Laclau and others 2005), and 1.2–3.0 kg N ha^{-1} y^{-1} in Venezuela (Chacon and others 1991).

Some studies on nitrogen cycling have assumed, albeit without presenting evidence, that nitrogen balances in savanna are neutral (Bate 1981; Sanhueza and Crutzen 1998; Laclau and others 2005). We found that in most of the savanna types N losses through fire would only be compensated by atmospheric deposition if the fire frequency were once every 3 years or less, whereas for P balances may be positive even at high fire frequency (Appendix D in Supplementary material). However, the losses through fire from very nutrient-rich vegetation types like the former paddocks can never be matched by inputs (Appendix D in Supplementary material). Input of N through symbiotic fixation is only substantial in *Acacia* woodlands; indeed, dense stands may have a positive N balance (Figure 7) provided that the fires do not burn the trees (not included in Figure 7; Appendix D in Supplementary material). Tall grass savanna, and particularly grazed patches, would need high non-symbiotic N$_2$-fixation rates to have a neutral N-balance (compare legend of Figure 7). Inputs of N and P through herbivore dung and urine appear to be significant only in the grazed patches (Figure 7; Appendix D in Supplementary material). Our results indicate that in such areas nutrient losses through biomass consumption by herbivores may be higher than inputs by dung and urine, possibly leading to negative balances for both N and P.

It is clear that one of the main effects of cattle ranching is to re-distribute large amounts of N and P, this effect being more persistent for P than for N. In the Mkwaja area, 50 years of cattle ranching created a heterogenous savanna landscape, with scattered, nutrient-rich patches in an otherwise nutrient-poor ecosystem. Similar effects of cattle have been observed in other parts of Eastern Africa (Stelfox 1986; Reid and Ellis 1995; Young and others 1995; Augustine 2003), where they also produce very distinct vegetation with *Cynodon*-dominated glades and surrounding bushes, as well as in Southern Africa, Australia, and the South America pampas. From an ecological point of view, these nutrient enriched patches can be thought of as novel ecosystems, having a species composition quite different from that of the surrounding vegetation, and often including several non-native species. In this respect, they contribute to the overall diversity of the landscape and, from the perspective of nature conservation, may even be beneficial. Such areas are often heavily used by wildlife, and may increase the numbers and diversity of wild herbivores that the larger area can support (Blackmore and others 1990; Young and others 1995; Augustine 2003; Treydte and others 2006b). It seems preferable, therefore, to maintain these nutrient hot-spots, rather than attempting to ''restore'' them, for example, by spreading soil from the former paddocks over the surrounding savanna. The latter would, in any case, increase the natural P pool more strongly than that of N, because so much N is lost through ammonia volatilization and leaching (compare Augustine 2003).

In an earlier article, we presented a conceptual framework for N and P stoichiometry in savanna ecosystems, postulating that frequent fires and excretion by herbivores lead to N-limitation, whereas N$_2$-fixation leads to P limitation (compare Cech and others 2008). The results presented here support this concept, and demonstrate that N and P balances calculated at smaller spatial scales can provide valuable insights into the functioning of savanna ecosystems. In addition, such information may help in improving management, for example, by detecting the early effects of overgrazing or reducing nutrient losses through fire.

ACKNOWLEDGMENTS

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