

## GRAZING OPTIMIZATION AND NUTRIENT CYCLING: POTENTIAL IMPACT OF LARGE HERBIVORES IN A SAVANNA SYSTEM

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**Abstract.** Using a model, we test the prediction that herbivory can result in grazing optimization of primary production in a nitrogen-limited system where large losses of nitrogen occur in annual fires. The model is based on the nitrogen budget of the humid savanna of Lamto, Ivory Coast, estimated from field data. At present, the ecosystem contains few herbivores, but buffalo and kob populations are increasing.

We show that grazing optimization through recycling of nitrogen would occur at Lamto in the short term (i.e., several decades) if the percentage of nitrogen lost from the system out of the amount ingested by herbivores is <24%, and in the long term (i.e., several centuries) if it is <19%. When 25% of nitrogen is lost by herbivores, primary production is maintained at a high level up to very high consumption rates. Because losses due to herbivores are likely to be lower than these values in this particular ecosystem, we conclude that grazing optimization is likely to occur in the Lamto savanna.

**Key words:** grazing optimization; herbivores' enhancement of primary production; herbivory; *Hyparrhenia diplandra*; Ivory Coast; *Kobus kob*; Lamto savanna; nitrogen budget; nitrogen cycle; nitrogen cycle model in a savanna ecosystem; primary production; *Syncerus caffer*.

### INTRODUCTION

The effects of herbivores on plant production are much debated in the literature (Dyer 1975, Dyer and Bokhari 1976, McNaughton 1976, Owen and Wiegert 1976, Stenseth 1978, McNaughton 1979, Hilbert et al. 1981, Owen and Wiegert 1981, McNaughton 1983, Belsky 1986, Dyer et al. 1986, McNaughton 1986, Belsky 1987, Paige and Whitham 1987, Westoby 1989, Belsky et al. 1993, Dyer et al. 1993, Milchunas and Lauenroth 1993, Bergelson et al. 1996, and others). The grazing optimization hypothesis (McNaughton 1979, Hilbert et al. 1981, Dyer et al. 1986) states that primary production or even plant fitness can increase with grazing intensity and reach a maximum at a moderate rate of herbivory. One possible explanation for the beneficial effect of herbivores on plant production is that they recycle a limiting nutrient and hence promote plant growth (Floate 1981, Cargill and Jefferies 1984a, Carpenter and Kitchell 1984, Bazely and Jefferies 1985, Dyer et al. 1986, Ruess and McNaughton 1987, Holland et al. 1992, Loreau 1995).

More precisely, some authors have suggested that a beneficial effect of herbivory through the recycling of a limiting nutrient comes from increased turnover rate (Floate 1981, Cargill and Jefferies 1984a, Bazely and Jefferies 1985, Dyer et al. 1986, Ruess and McNaughton 1987, Loreau 1995). In a previous paper (de Ma-

zancourt et al. 1998), we showed that grazing optimization hinges on losses of the limiting nutrient and not on its turnover rate in an ecosystem at steady state. We define the "herbivore pathway" as that part of the plant nutrient stock that is consumed by herbivores and the "plant pathway" as the remaining plant nutrient stock that is not consumed by herbivores. We further define the fraction of nutrient lost along either of these pathways as the amount of nutrient lost from the ecosystem during nutrient cycling divided by the total amount of nutrient that passes through these pathways. Grazing optimization then requires that (1) the proportion of nutrient lost along the herbivore pathway be smaller than the proportion of nutrient lost throughout the plant pathway, and (2) the inputs of nutrient to the system be sufficient and plant uptake rate be sufficiently sensitive to an increase in soil mineral nutrient concentration (de Mazancourt et al. 1998). Consequently, grazing optimization is most likely to occur in systems with large losses of the limiting nutrient during recycling of plant detritus.

This is the case in the humid savanna of Lamto, Ivory Coast, Africa, where the main limiting nutrient, nitrogen, is subject to large losses during recycling of plant detritus in annual fires. Here, we explore the likelihood of grazing optimization in this savanna ecosystem. We first use field data on nutrient stocks and fluxes to build a model of the nitrogen cycle. Using this model, we then address the potential impact of the recent increase of large herbivorous mammal populations on the nitrogen cycle and plant production, and we determine the maximal losses of nitrogen by herbivores that could allow grazing optimization. Finally, we discuss the

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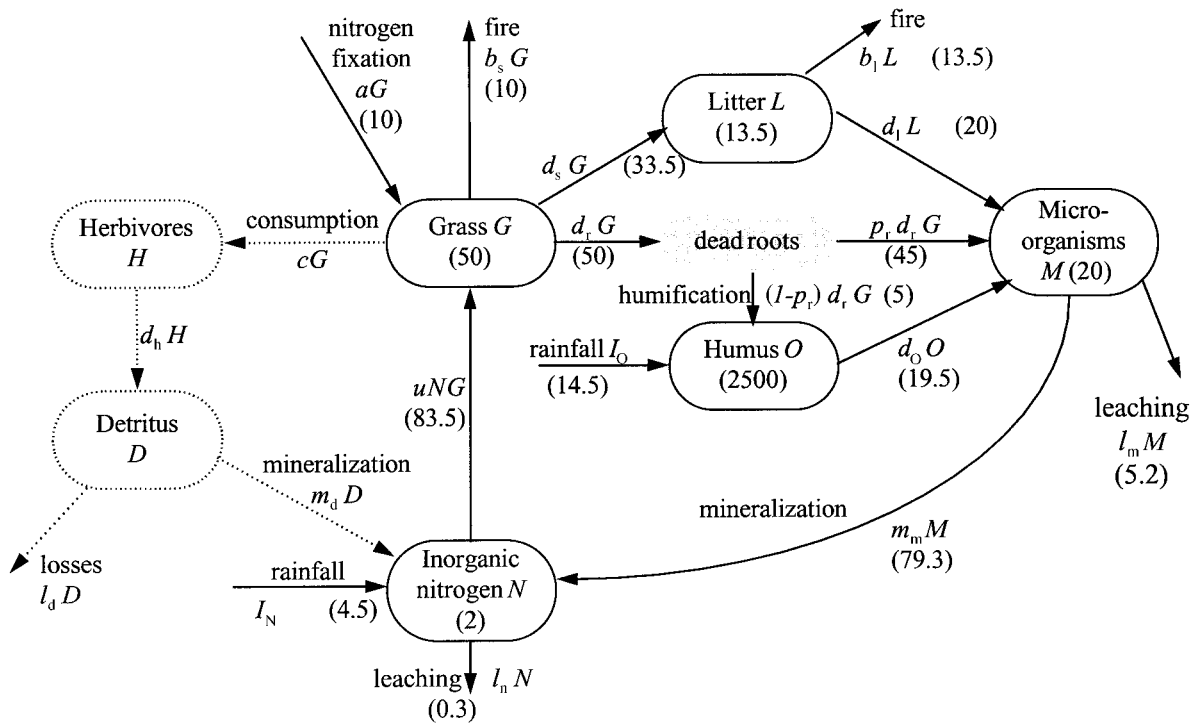


FIG. 1. Model of the nitrogen cycle in the humid savanna of Lamto, Ivory Coast. In the present ecosystem, herbivores are virtually absent (consumption  $\approx 0$ ). Estimates of the stocks (in kg N/ha) and fluxes (in kg N·ha<sup>-1</sup>·yr<sup>-1</sup>) in the present ecosystem are in parentheses. The mean residence times of nitrogen in the various compartments are as follows: inorganic nitrogen, 9 d (0.024 yr); microorganisms, 3 mo (0.24 yr); litter, 5 mo (0.4 yr); grass, 6 mo (0.53 yr); humic stock, 130 yr.

likelihood of grazing optimization using data from the literature.

THE LAMTO ECOSYSTEM

The Lamto savanna (5°02' W, 6°13' N; 200 km north of Abidjan, Ivory Coast) has been investigated for 35 yr by the Laboratory of Ecology (Paris, France) and is one of the best studied ecosystems in the world. It lies in the Guinean bioclimatic zone, close to the West African rain forest. Savannas are intersected by fringing forests along the intermittent rivers and by remnants of the semideciduous forest on the plateaus (Devineau 1975). Monthly mean temperatures range 25–28°C. Annual rainfall is ~1200 mm, and has a bimodal distribution (Lecordier 1974). The long dry season occurs in December and January. Fire occurs during this dry season (in January), removing all standing biomass and the nitrogen it contains. It is a major source of nitrogen loss in this ecosystem (Abbadie 1990). A short dry season occurs in August.

Until recently, large herbivores were virtually absent from the Lamto savanna (Bourlière et al. 1974, Lamotte 1982) and were systematically neglected in ecological studies. At Lamto, buffalo (*Syncerus caffer*) and Buffon's kob (*Kobus kob*) populations were estimated at 10 and 20–30 individuals, respectively, in 1974 (Bourlière et al. 1974). Their populations have been increas-

ing during the last decade (Glemin 1996). Glemin (1996) estimated kob and buffalo populations to 60 individuals each in 1996, which amounts to a mean density of 2.5 individuals/km<sup>2</sup>. Here, we assess their possible impact on nitrogen cycling and plant productivity in this ecosystem.

Several vegetation types can be differentiated in Lamto, depending on shrub density (César 1971, Menaud and César 1979, Gautier 1990). Here we consider the *Andropogonae* open shrub savanna, dominated by the grass *Hyparrhenia diplandra*, which is the most studied type of vegetation.

We investigate the nitrogen cycle because nitrogen is likely to be limiting in this savanna, as it is in many ecosystems (Vitousek and Howarth 1991). Keya (1973) showed that primary productivity, in terms of both biomass production and protein production, increased linearly with nitrogen additions up to 300 kg N/ha in a dry *Hyparrhenia* savanna in Kenya. In a humid *Trachypogon* savanna in Venezuela, fertilization experiments showed that nitrogen was the major limiting nutrient (Medina et al. 1978). At Lamto, C<sub>4</sub> grasses maintain a high photosynthetic capacity with a low leaf nitrogen content (Le Roux and Mordelet 1995). Low leaf nitrogen content is common in humid oligotrophic savannas (Medina et al. 1978, Abbadie 1984) and indicates that nitrogen is a major limiting factor.

TABLE 1. Parameters of the model.

Parameter	Estimated value and dimension	Definition
General model parameters		
$I_N$	4.5 kg N·ha <sup>-1</sup> ·yr <sup>-1</sup>	Annual mineral nitrogen input from rainfall.
$I_O$	14.5 kg N·ha <sup>-1</sup> ·yr <sup>-1</sup>	Annual organic nitrogen input from rainfall.
$l_n$	0.15 yr <sup>-1</sup>	Annual mineral nitrogen leaching rate.
$u$	0.835 kg N·ha <sup>-1</sup> ·yr <sup>-1</sup>	Annual rate of mineral nitrogen uptake by grass per unit $G$ and $N$ .
$a$	0.2 yr <sup>-1</sup>	Annual atmospheric nitrogen assimilation rate of rhizospheric bacteria per unit $G$ .
$b_s$	0.2 yr <sup>-1</sup>	Annual burning rate of living shoot per unit $G$ (shoot plus root nitrogen in November).
$d_s$	0.67 yr <sup>-1</sup>	Annual plant death rate corresponding to shoot mortality.
$b_l$	1 yr <sup>-1</sup>	Annual burning rate of litter nitrogen.
$d_l$	1.48 yr <sup>-1</sup>	Annual decomposition rate of litter nitrogen.
$d_r$	1 yr <sup>-1</sup>	Annual plant death rate corresponding to root mortality.
$p_r$	0.9	Proportion of dead root nitrogen directly decomposed by microorganisms.
$d_O$	7.810 <sup>-3</sup> yr <sup>-1</sup>	Annual decomposition rate of the humic stock.
$m_m$	3.965 yr <sup>-1</sup>	Annual mineralization rate by microorganisms.
$l_m$	0.26 yr <sup>-1</sup>	Annual organic nitrogen leaching rate.
Herbivore parameters		
$c$	yr <sup>-1</sup>	Annual rate of grass consumption by herbivores.
$d_h$	yr <sup>-1</sup>	Annual rate of detritus production by herbivores.
$m_d$	yr <sup>-1</sup>	Annual mineralization rate of herbivore detritus.
$l_d$	yr <sup>-1</sup>	Annual nitrogen loss rate of herbivore detritus.

## MODEL DESCRIPTION AND DATA

Our model of the Lamto nitrogen cycle has seven compartments (Fig. 1). All stocks and fluxes are expressed in units of nitrogen (kg N/ha, kg N·ha<sup>-1</sup>·yr<sup>-1</sup>) and represent annual means.

Five compartments describe the present ecosystem. Primary producers are represented by the grass compartment  $G$ . Grass takes up nitrogen from the pool of soil mineral nitrogen  $N$ . Dead grass shoots supply the litter  $L$ . Dead grass roots are either directly decomposed by soil microorganisms  $M$ , or go to the humic stock  $O$ . Microorganisms  $M$  decompose organic matter from litter, dead roots, and humic stock, and they supply the soil mineral nitrogen  $N$  by mineralization. The “plant pathway” describes the fate of that part of the plant nitrogen stock that is not consumed by herbivores: it may pass through the litter or humic stock and microorganism compartments, or it may be lost by fire or leaching.

The other two compartments describe what we term the “herbivore pathway”: herbivores  $H$  consume grass and produce detritus  $D$  (excrements and corpses). This detritus might be decomposed partly by the same microorganisms that act upon plant detritus. However, because the dynamics of mineralization and leaching for these two types of detritus are different, they are represented in the model by separate pathways.

Inputs of nitrogen into the system come mainly from rainfall, with deposition of mineral,  $I_N$ , and organic,  $I_O$ , nitrogen. Some atmospheric nitrogen is also assimilated by rhizospheric bacteria (see the Appendix). Outputs occur mainly through fire, which removes nitrogen from living shoots and litter, and through leaching of mineral and organic nitrogen.

To minimize the number of parameters, we chose

simple functions for fluxes between compartments. The equations are as follows:

$$\frac{dG}{dt} = uNG + aG - b_sG - d_sG - d_rG - cG \quad (1)$$

$$\frac{dH}{dt} = cG - d_hH \quad (2)$$

$$\frac{dD}{dt} = d_hH - l_dD - m_dD \quad (3)$$

$$\frac{dL}{dt} = d_sG - b_lL - d_lL \quad (4)$$

$$\frac{dO}{dt} = (1 - p_r)d_rG + I_O - d_OO \quad (5)$$

$$\frac{dM}{dt} = d_lL + p_r d_rG + d_OO - l_mM - m_mM \quad (6)$$

$$\frac{dN}{dt} = m_dD + m_mM + I_N - l_nN - uNG. \quad (7)$$

All parameters, their dimensions and their definitions are summarized in Table 1.

Most functions describe linear, donor-controlled interactions. For example, all the detritus compartments (litter, humic stock, microorganisms, and herbivore detritus) are assumed to be resource-controlled; the fraction of resource decomposed does not depend on decomposer abundance.

Grass uptake is assumed to be proportional to grass root biomass, hence to grass nitrogen stock  $G$  (assuming a constant root/shoot ratio) and to soil mineral nitrogen  $N$ ; thus grass uptake has the form  $uNG$ . Atmospheric nitrogen assimilated by rhizospheric bacteria is assumed to go to the grass compartment. This

amount is assumed to have the form  $aG$ , i.e., rhizospheric bacteria activity is proportional to the amount of root exudates (Balandreau 1976), hence of photosynthates, which we assume to be proportional to the grass nitrogen stock  $G$ .

The plant–herbivore interaction is a donor-controlled trophic function, i.e., the consumption function depends on grass only. We chose the simplest donor-controlled trophic function, proportional to the grass compartment,  $cG$ , because we showed (de Mazancourt et al. 1998) that grazing optimization is independent of the particular trophic function chosen. The rate of grass consumption by herbivores,  $c$ , is a measure of grazing intensity.

We established the nitrogen budget for the present ecosystem without herbivores (Fig. 1). These data come either from the literature on the Lamto savanna or from unpublished measurements (detailed in the Appendix). All parameters that do not concern herbivores (Table 1) were then estimated from this budget, assuming that the ecosystem is in a steady state.

The model assumes that grazing changes neither natural shoot and root death rates,  $d_s$  and  $d_r$ , nor the rate of loss to fire,  $b_s$ . This amounts to assuming that consumption by herbivores does not change the grass shoot–root balance. This might not be the case for the Lamto grasses, but plant regrowth after defoliation is unpredictable (McNaughton 1979, Kotanen and Jefferies 1987, van der Meijden et al. 1988, Bazely and Jefferies 1989). Moreover, herbivores can change the species composition of vegetation (McNaughton 1985, Bazely and Jefferies 1986). In dry savanna ecosystems, overgrazing can result in encroachment by bush (Walker et al. 1981). A change in the species composition is expected with the arrival of large herbivores, but it cannot be modeled in the present state of knowledge.

RESULTS

*Equilibrium analysis*

The analysis of the model gives the following equilibrium grass biomass  $G^*$  and primary production  $\Phi^*$  in terms of nitrogen:

$$G^* = \frac{S_n - I_n N^*}{m_p \beta_p + c \beta_h} \tag{8}$$

$$\Phi^* = u N^* G^* + a G^* = \frac{S_n - I_n N^*}{\beta_t} \tag{9}$$

where  $S_n$  is the net nitrogen input in the ecosystem,  $I_n N^*$  represents leaching of mineral nitrogen,  $m_p$  is the rate of plant detritus production,  $\beta_p$  is the fraction of nitrogen lost along the plant pathway,  $\beta_h$  is the fraction of nitrogen lost along herbivore pathway, and  $\beta_t$  is the fraction of nitrogen lost along both pathways. The equations for these lumped parameters are in Table 2.

Primary production at equilibrium  $\Phi^*$  reaches zero when grazing intensity  $c$  reaches a maximum value,

denoted as  $c_{\max}$ . At this point, leaching of mineral nitrogen is equal to net nitrogen input in the ecosystem:

$$c_{\max} = \frac{u}{I_n} \left( S_n - I_n \frac{m_p}{u} \right) \tag{10}$$

The percentage of primary production consumed by herbivores is linked to grazing intensity according to the following formula:

$$x = \frac{c}{c + m_p} \times 100. \tag{11}$$

With the present data, primary production reaches zero when herbivore consumption is 98% of primary production.

The condition for grazing optimization to occur at equilibrium is given by

$$\left( \frac{d\Phi^*}{dc} \right)_{c=0} > 0 \tag{12}$$

which is obtained when

$$\beta_h < \beta_p \left( 1 - \frac{I_n N_0^*}{S_n - I_n N_0^*} \right) \tag{13}$$

(de Mazancourt et al. 1998). With the present data, this condition is  $\beta_h < 0.19$ . Thus, less <19% of the nitrogen that passes through the herbivore pathway must be lost from this pathway for grazing optimization to occur at equilibrium.

*Herbivore production*

Fig. 2a shows the herbivore consumption (percentage of primary production consumed by herbivores) that maximizes either primary production or herbivore production as a function of the fraction of nutrient lost along the herbivore pathway. Herbivore consumption, which is here equal to herbivore production, is maximized for a greater grazing intensity than is plant production (Fig. 2a). The optimal percentage of consumption for herbivore production is high (>80%), whatever the fraction of nitrogen lost along the herbivore pathway.

Fig. 2b shows herbivore optimal production as a function of the fraction of nitrogen lost along the herbivore pathway. Herbivore production is a decreasing function of the fraction of nitrogen lost along the herbivore pathway.

In terms of livestock management, this means that a high level of consumption maximizes herbivore production. Nevertheless, the production that is of interest to livestock management is the amount of animals removed from the system for meat production. Animal removal is an additional loss along the herbivore pathway; hence, it decreases both primary production and herbivore production (Fig. 2b).

*Dynamic analysis*

This equilibrium analysis indicates the trend of the system after a time sufficient to reach steady state. We

TABLE 2. Lumped parameters of the models.

Parameter	Units	Meaning and equation
$S_n$	kg N · ha <sup>-1</sup> · yr <sup>-1</sup>	Net nitrogen input in the system $S_n = I_N + I_O \left( \frac{m_m}{m_m + l_m} \right)$
$N^*$	kg N/ha	Equilibrium soil nitrogen $N^* = \frac{m_p + c}{u}$
$N_0^*$	kg N/ha	Equilibrium soil nitrogen in the system without herbivores $N_0^* = \frac{m_p}{u}$
$\beta_p$	dimensionless	Fraction of nitrogen lost along the plant pathway $\beta_p = \frac{b_s - a + d_s \left( \frac{b_1}{b_1 + d_1} + \frac{d_1}{b_1 + d_1} \frac{l_m}{l_m + m_m} \right) + d_r \frac{l_m}{l_m + m_m}}{m_p}$
$\beta_h$	dimensionless	Fraction of nitrogen lost along the herbivore pathway $\beta_h = \frac{l_d}{l_d + m_d}$
$\beta_t$	dimensionless	Fraction of nitrogen lost along both plant and herbivore pathways $\beta_t = \frac{m_p \beta_p + c \beta_h}{m_p + a + c}$
$x$	dimensionless	Percentage of primary production consumed by herbivores $x = \frac{c}{c + m_p} \times 100$
$m_p$	yr <sup>-1</sup>	Rate of plant detritus production $m_p = b_s - a + d_s + d_r$

can find indications of the time scale of transient dynamics from the mean residence times of nitrogen in the various compartments. These are obtained by dividing a compartment's nitrogen stock by either its total nitrogen input or its total nitrogen output at steady state (Fig. 1). These residence times are all <1 yr except for the humic stock, in which mean nitrogen residence time is ~130 yr. Fig. 3 shows the results of a simulation where herbivores are introduced at time  $t = 0$ , displaying annual means of grass biomass and primary production as functions of time. The equilibrium of the system is only reached after several times the longest mean residence time, i.e., several centuries (Fig. 3). If we are interested in the trends of the system on a much shorter time scale, for example two decades, we may make the approximation that the humic stock stays constant during this period. The system is then equivalent to the simplified system represented in Fig. 4. Fig. 5 shows the dynamics of the system during two decades. The trends of the system on such a shorter time scale are given by the equilibrium analysis of this new sys-

tem (Fig. 5). Grazing optimization of this simplified system, on a short time scale, occurs if  $\beta_h < 0.24$ . Thus, grazing optimization is obtained in the relatively short term (i.e., several decades) if the percentage of nitrogen ingested by herbivores that is lost from the system on its way to the mineral stock is <24%, which is a slightly higher value than in the long-term equilibrium.

#### Sensitivity analysis

Primary production and grass biomass as a function of grazing intensity are sensitive to the fraction of nitrogen lost along the herbivore pathway,  $\beta_h$  (Fig. 6). Note that when <25% of the nitrogen ingested by herbivores is lost, primary production is increased or maintained up to a high consumption level.

Plant biomass is a linearly decreasing function of grazing intensity when  $\beta_h = 0$ . For a low percentage of consumption (Eq. 11), an increase in the percentage of consumption corresponds to a slow increase of grazing intensity. Hence, for low percentages of consumption, the decrease of primary production with con-

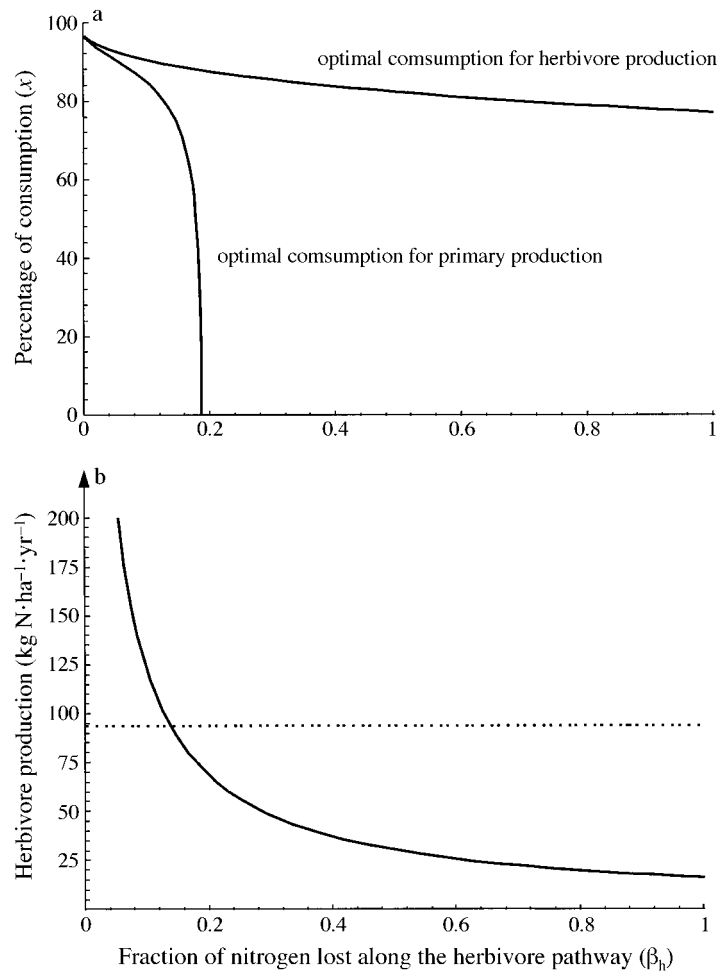


FIG. 2. (a) Percentage of primary production consumed by herbivores that maximizes primary production and herbivore production as a function of the fraction of nitrogen lost along the herbivore pathway. (b) Herbivore production at the consumption rate that maximizes herbivore production, as a function of the fraction of nitrogen lost along the herbivore pathway. The dotted line is primary production in the absence of herbivore consumption (consumption rate is zero).

sumption is slow. On the other hand, for a high percentage of consumption, an increase in the percentage of consumption corresponds to a large increase of grazing intensity. Hence, for high percentages of consumption, the decrease of primary production with consumption is steep. The scale of the percentage of consumption thus explains why we find primary production maintained up to high levels of consumption.

#### DISCUSSION

Grazing optimization through recycling of nitrogen is expected to occur in the Lamto savanna in the short term (i.e., several decades) if the percentage of nitrogen ingested by herbivores that is lost from the system is  $<24\%$ , and in the long term, i.e., several centuries, if it is  $<19\%$ . Furthermore, at  $<25\%$  of nitrogen lost by herbivores, primary production is expected to be maintained at a high level, or increased, up to high consumption rates (80–90% of primary production consumed).

In the Lamto savanna, where large losses of nitrogen occur in annual fires, herbivores reduce the nitrogen loss by fire, because they reduce grass biomass. This

effect of herbivores on the amount of nitrogen lost by fire was shown experimentally in a tallgrass prairie in Kansas, USA (Hobbs et al. 1991). Large herbivores are likely to be safe from fire, and thus keep more nitrogen in the ecosystem. Smaller herbivores such as insects may burn, and this should be taken into account in the fraction of nitrogen lost along the herbivore pathway. The net effect of herbivores on the nitrogen cycle and primary production also depends on the fate of the nitrogen they ingest. Their effect can be positive only if they recycle a sufficient proportion of nitrogen in the system, as we showed with the present model.

#### *Losses of nitrogen due to large herbivores*

The role of herbivores as fertilizers through urine and feces has been seriously questioned for some decades. Several authors (Denmead et al. 1974, Woodmansee et al. 1981, Ryden et al. 1984) even suggested that herbivores are a major pathway of nitrogen losses in grasslands. Urine is a concentrated solution deposited on a small area, and urine patches are likely to contain nitrogen in excess of plant demand. Under such conditions, the retention of nitrogen might be reduced,



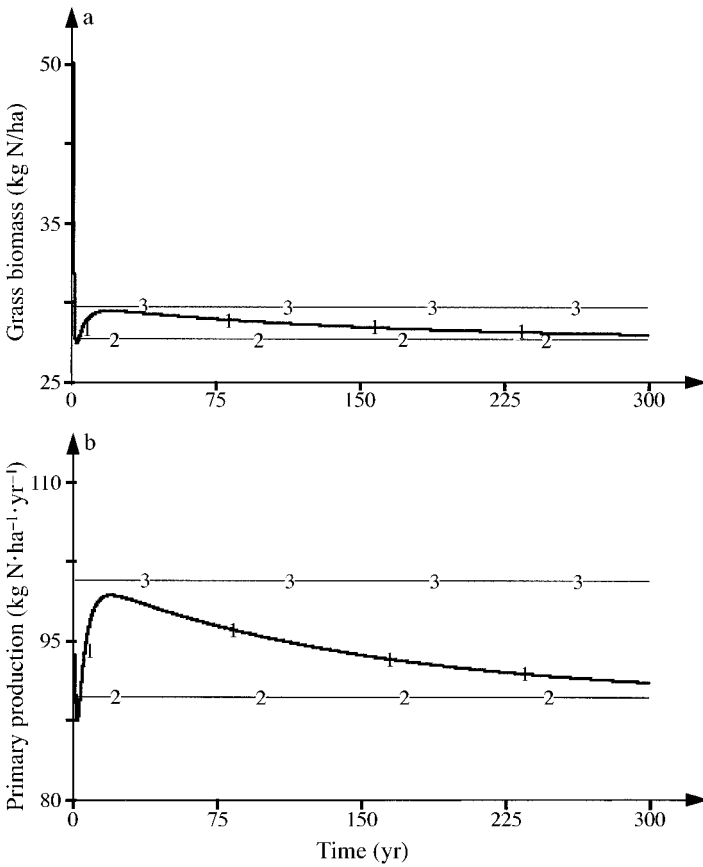


FIG. 3. Dynamics of the system of Fig. 1: (a) grass biomass  $G$  as a function of simulation time; (b) primary production  $\Phi$  as a function of simulation time. At  $t = 0$ , the system is at the equilibrium without herbivores. Grazing is introduced with a grazing intensity of  $c = 1.87 \text{ yr}^{-1}$ , e.g., 50% of primary production consumed by herbivores, and a 20% loss of nitrogen along the herbivore pathway ( $\beta_h = 0.2$ ). Curves (1) show dynamics of the system of Fig. 1; lines (2) show equilibrium values of the system of Fig. 1; lines (3) show equilibrium values of the simplified system of Fig. 4.

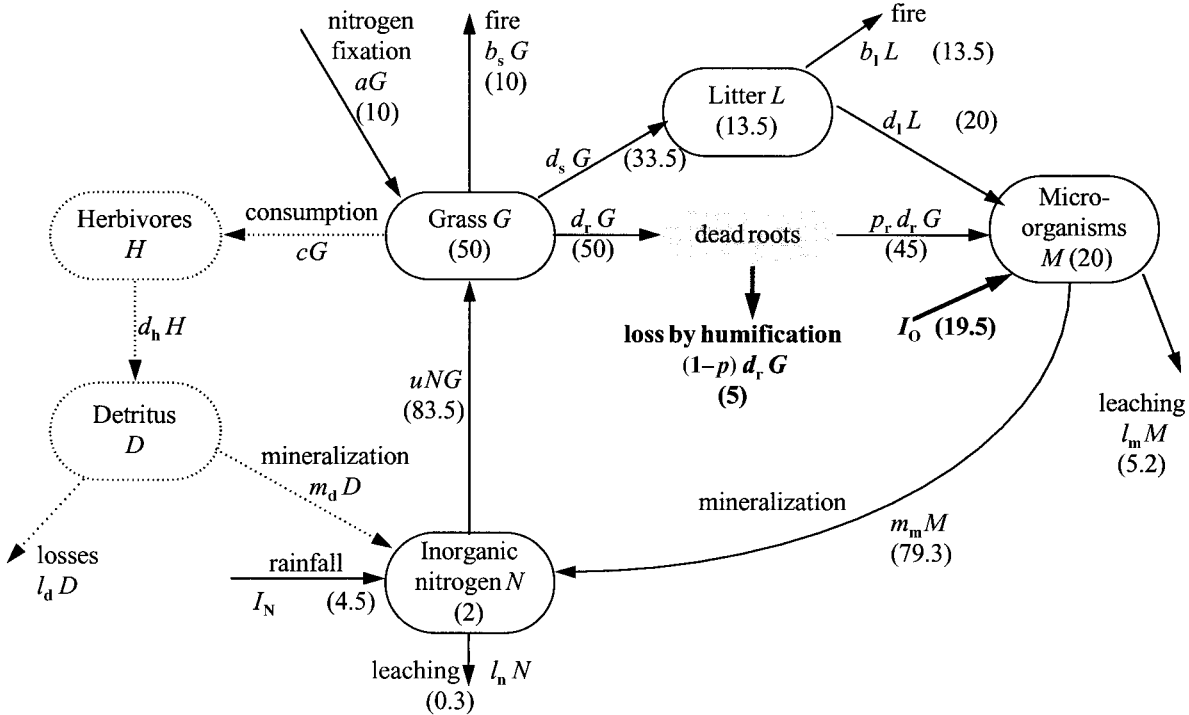
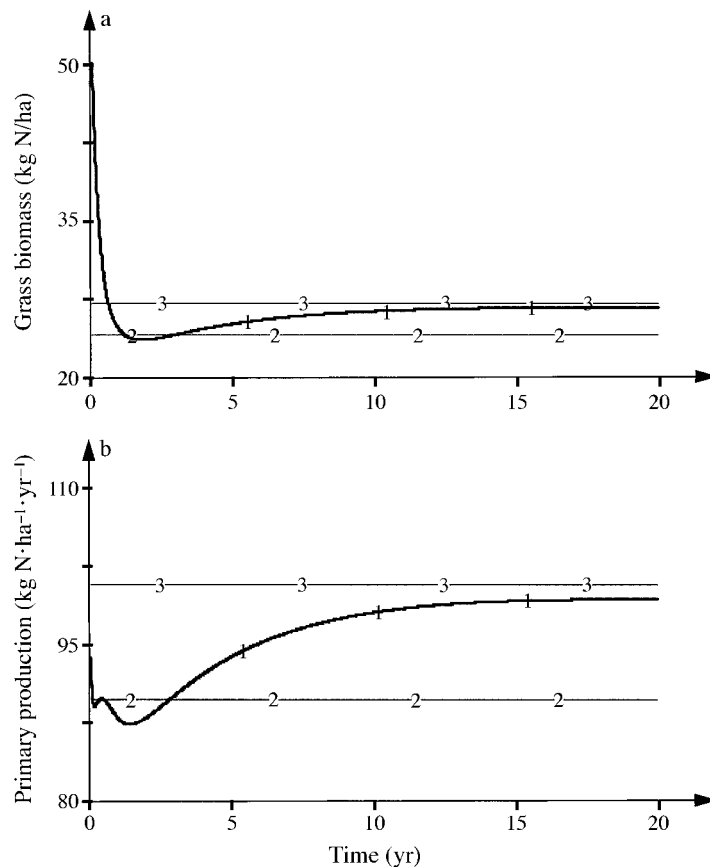


FIG. 4. Simplified system for the analysis on a short time scale. Dead roots going to the humic compartment are considered lost for the system. The humic compartment is assumed to stay constant, resulting in a constant input to the bacterial compartment.

FIG. 5. Dynamics of the system of Fig. 1 on a short time scale: (a) grass biomass  $G$  as a function of simulation time; (b) primary production  $\Phi$  as a function of simulation time. At  $t = 0$ , the system is at the equilibrium without herbivores. Grazing is introduced with a grazing intensity of  $c = 1.87 \text{ yr}^{-1}$ , e.g., 50% of primary production consumed by herbivores, and a 20% loss of nitrogen along the herbivore pathway ( $\beta_h = 0.2$ ). Curves (1) show dynamics of the system of Fig. 1; lines (2) show equilibrium values of the system of Fig. 1; lines (3) show equilibrium values of the simplified system of Fig. 4. The equilibrium value of the simplified system of Fig. 4 gives the trend of the entire system on a time scale of decades.



with losses occurring through various processes, such as leaching, denitrification, and ammonia volatilization following urea hydrolysis (Langford et al. 1992). Several studies reported the amount of nitrogen applied in the form of urine that is recovered in the vegetation and the soil after several weeks. They measured losses of 40–75% of the urine-applied nitrogen (Ball et al. 1979, Carran et al. 1982, Vallis et al. 1985, Pakrou and Dillon 1995). Losses through each of the three processes have also been measured in different systems, mainly in sheep and cattle pastures or in the laboratory. Between 2 and 12% of the nitrogen was lost by leaching (Williams and Haynes 1994, Pakrou and Dillon 1995); 0–13% of the applied nitrogen was lost by denitrification (Monaghan and Barraclough 1993, Pakrou and Dillon 1995); and 0–40% of the applied nitrogen by ammonia volatilization, with a mean of ~18% (Musa 1968, Denmead et al. 1974, Ball et al. 1979, Carran et al. 1982, Vallis et al. 1982, Bouwmeester et al. 1985, Schimel et al. 1986, Ruess and McNaughton 1988, Jarvis et al. 1989, Lockyer and Whitehead 1990, Whitehead and Raistick 1991, Whitehead and Raistick 1992, Whitehead and Raistick 1993, Pakrou and Dillon 1995, Frank and Zhang 1997). Woodmansee et al. (1981) reported much higher values of volatilization: ~50–80%. The amount of ammonia volatilization, however, is highly dependent on fertilization (Jarvis et al. 1989),

season (Vallis et al. 1982), humidity (Musa 1968, Carran et al. 1982), type of herbivores (Ball et al. 1979), grazing intensity (Ruess and McNaughton 1988), temperature (Whitehead and Raistick 1991), soil cation exchange capacity (Whitehead and Raistick 1993), plant cover (Ruess and McNaughton 1988, Whitehead and Raistick 1992), and wind (Bouwmeester et al. 1985).

The conclusions of these studies are contradictory. Some authors concluded that herbivores have a strong impact on nitrogen losses, mostly in intensive pastoral systems. Schimel et al. (1986), on the contrary, concluded that losses due to volatilization of ammonia from urine patches were an order of magnitude lower than the losses due to volatilization of ammonia from senescent vegetation in an American grazed pasture. Ruess and McNaughton (1988) concluded that large herbivores contribute to nutrient conservation in the Serengeti savanna. From their study on ungulates in the Yellowstone National Park (USA), Frank and Zhang (1997) also concluded that these do not have a negative impact on soil nitrogen.

In the Lamto ecosystem, small losses through ammonia volatilization are expected because of the low soil pH (~5.5–6). Small losses through denitrification are also expected, because the denitrification potential is low in the Lamto savanna (Abbadie and Lensi 1990,



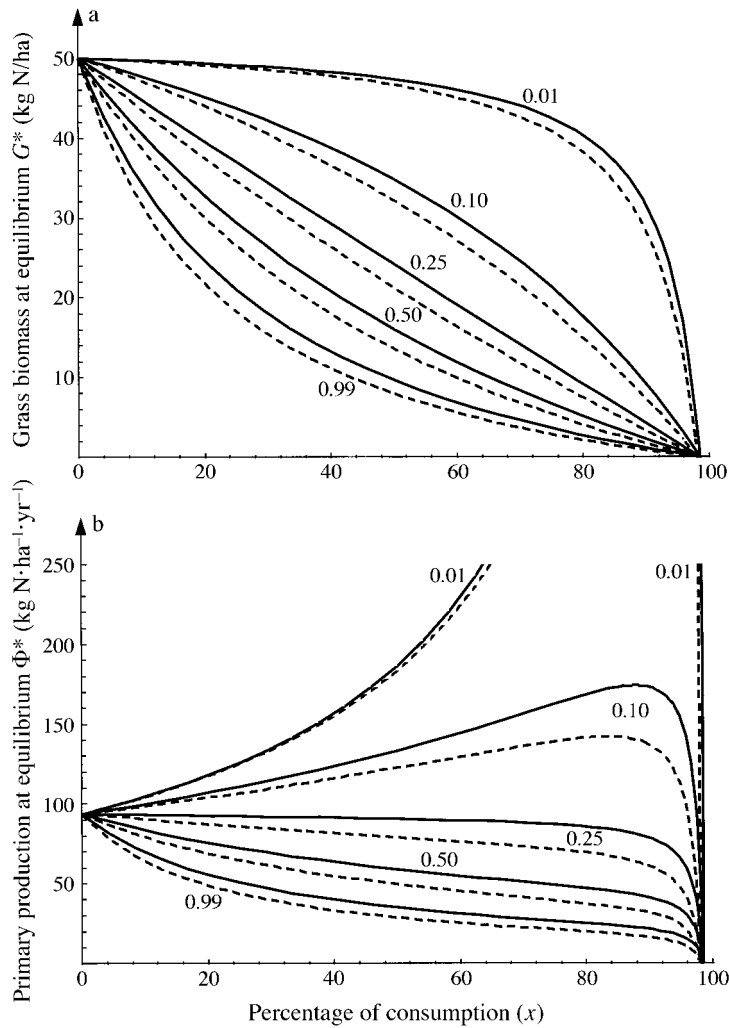


FIG. 6. (a) Equilibrium grass biomass and (b) primary production as functions of the percentage of primary production consumed by herbivores, at five fractions of nitrogen losses by herbivores:  $\beta_h = 0.01$ ,  $\beta_h = 0.10$ ,  $\beta_h = 0.25$ ,  $\beta_h = 0.50$ , and  $\beta_h = 0.99$ . Solid lines represent trend on a short time scale (decades) given by the equilibrium of the simplified system of Fig. 4. Dashed lines represent trend of the system on a long time scale (centuries) given by the equilibrium of the entire system of Fig. 1.

Lensi et al. 1992). Thus, losses induced by herbivores are likely to be smaller at Lamto than in some other savannas.

Between 50 and 75% of the nitrogen released by large herbivores is in the form of urine, depending on forage quality (Woodmansee et al. 1981, Ruess and McNaughton 1988, Jarvis et al. 1989) and season (Frank et al. 1994), whereas the amount of fecal nitrogen stays constant. Roughly 85% of urine nitrogen is in the form of urea (Ruess and McNaughton 1988), which is subject to losses by volatilization as we have described. Therefore, the threshold values of 19 and 24% are reasonable mean figures of nitrogen losses due to herbivores, according to the literature. Smaller losses are likely to occur in the Lamto system, and, therefore, grazing optimization is likely to occur in this ecosystem. A field study will allow us to measure losses of nitrogen linked with herbivores in the Lamto savanna and to assess their effect on the nitrogen cycle and primary production.

There is still a lack of knowledge of the conditions

where herbivores can be expected to result in large losses of nitrogen. Sheep have been shown to result in lower losses, as they urinate smaller amounts and more often than do cattle (Ball et al. 1979). Smaller herbivores can be expected to induce lower losses. Losses linked with insect herbivores have not been assessed, but might be much lower because insects excrete only solid material (Raven and Johnson 1996).

#### *The effect of patchy urine and dung deposition*

As urine and dung are deposited on small areas, we can expect that the spatial heterogeneity they introduce will have a significant effect on primary production. This is a limitation of our model, because it assumes a homogeneous distribution of plants, herbivore consumption, and excreta.

Lotero et al. (1966) measured the area fertilized by urination and the duration of the effect. They concluded that urine that was returned by grazing cattle contributed little to the fertility of the pasture as a whole. Gillingham and During (1973) showed that herbivores

transferred nitrogen and potassium from some parts of a pasture to other parts, resulting in net losses of nitrogen from some areas (the least productive two thirds of the paddock) and net gains for camp areas. Hilder (1966; cited by Gillingham and During [1973]) found that one-third of the sheep dung was concentrated on <5% of a flat paddock, and urine distribution seemed similar.

#### *Other effects of herbivores*

Herbivores have many different effects on plants, beyond the nitrogen cycle. Herbivores affect plants by trampling, they induce physiological changes, and they change competition parameters between species (Huntly 1995). Plant regrowth after defoliation is unpredictable, depending on numerous factors (McNaughton 1979, Kotanen and Jefferies 1987, van der Meijden et al. 1988, Bazely and Jefferies 1989). Herbivores can also alter plant species composition (McNaughton 1985, Bazely and Jefferies 1986, Milchunas and Lauenroth 1993, Pastor and Cohen 1997). We have also studied the effects of plant species replacement (de Mazancourt and Loreau, *unpublished manuscript*). Some effects, e.g., trampling, can inhibit primary production, and others, such as reduction of self-shading or water stress, can be positive. Nevertheless, the effects of herbivores on the nitrogen cycle are important, as the following examples show.

#### *Consumption rates and grazing optimization*

In grasslands, herbivores typically consume 15–60% of the annual aboveground net primary production (Detling 1988). Some ecosystems, such as the Serengeti (Tanzania) and the La Pérouse Bay (Canada), sustain high loads of herbivory.

In the Serengeti savanna, large herbivores consume 17–94% of shoot production, with a mean of 60%. They consistently increase primary production, as measured by aboveground biomass production compared with enclosed sites without herbivores. Furthermore, they induce an increase in plant nitrogen content, when compared with ungrazed plants, by maintaining the grass in an immature, nitrogen-rich state (McNaughton 1985). Primary production, as measured by nitrogen productivity, seems to be enhanced by herbivores up to high consumption rates. In this system, primary production is nitrogen limited (McNaughton 1985). Ruess and McNaughton (1988) showed that herbivores contribute to nutrient conservation in this system. Thus, the increase of primary production observed with herbivory might in part be explained by the mechanism of recycling of limiting nitrogen.

In La Pérouse Bay in Canada, Lesser Snow Geese consumed 60–89% of shoot production, with a mean of 80% (Cargill and Jefferies 1984a, Bazely and Jefferies 1989). Lesser Snow Geese increased shoot productivity by 30–80% compared with enclosed sites. They also increased shoot nitrogen content. Primary

productivity is nitrogen limited (Cargill and Jefferies 1984b), and a mechanism of optimization through nitrogen cycling is likely (Bazely and Jefferies 1985, Hik and Jefferies 1990). However, 90% of plant biomass is below ground, and simple reallocation cannot be excluded. Moreover, although geese may have a positive effect on primary production through nitrogen cycling, they also seem to have a negative effect through a different process. Snow Geese grub for roots and rhizomes of salt marsh graminoids. This is followed by an increase of evaporation from sediments beneath disturbed swards, resulting in high soil salinity that adversely affects the growth of the remaining grazed plants (Srivastava and Jefferies 1996).

#### *Plant–herbivore coevolution*

The fact that grazing optimization can occur does not necessarily imply that it does occur. The question of the evolution of plant palatability is a completely different question, which is much debated in the literature (Owen and Wiegert 1981, Vail 1992, Belsky et al. 1993, Mathews 1994). Belsky et al. (1993) find it hard to imagine that there could be selection in plants to favor grazing. If recycling is spread over the whole plant population, a nonpalatable plant should always be favored since it benefits from nutrient cycling without suffering from any herbivory (Westoby 1989). However, we show in another paper (de Mazancourt and Loreau, *in press*) that the spatial heterogeneity induced by the plant–herbivore interaction can lead to selection for plant palatability.

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## APPENDIX

### MODEL DATA

All model parameters (Table 1) were estimated from data on current stocks and fluxes, assuming that the ecosystem is in an equilibrium state. The grazers (consumers of live plant material) currently present in the savanna, mainly insects and rodents and few large herbivores, were not taken into consideration. The quantity of live material ingested in the Lamto ecosystem could be <1% of the primary production (Lamotte 1977, 1982). Plant material is mainly consumed by detritivores such as termites. Data on several compartments, such as shoot and root nitrogen stocks and the amount of burned matter, fluctuate widely within and among years. Therefore, we used approximate mean values.

As tree and shrub primary production is much less than grass primary production in this savanna (Menaut and César 1979), and buffaloes and kobs are not browsers, we ignored trees and shrubs. This avoids including interactions between grass and trees that are not fully understood. We did not analyze successional phenomena that can be linked to the arrival of herbivores (Walker et al. 1981, Menaut et al. 1990, Hochberg et al. 1994, Jeltsch et al. 1996).

Grass shoots grow until November, then senesce until January. We represent the maximum shoot nitrogen stock, which corresponds to the maximum shoot biomass in November. We chose this maximum rather than the mean stock of shoot nitrogen because the latter was difficult to evaluate from literature data. Maximum shoot biomass is often used to characterize forage productivity (César 1992). Abbadie (1984) estimated maximum shoot nitrogen stock to be 20 kg N/ha, which is consistent with the estimates by Menaut and César (1979) and César (1992). Abbadie (1984) also reported 17 kg N/ha for the mean root nitrogen stock. César (1971) and Menaut and César (1979) estimated root biomass as 10 000-14 000 kg/ha. Root nitrogen content was estimated at 0.3% of dry matter by Abbadie (1984) and 0.44-0.54% by César (1992). These figures put root nitrogen stock in a range 17-70 kg N/ha. We used a value of 30 kg N/ha. The grass nitrogen compartment was thus estimated at 50 kg N/ha (shoots, 20 kg N/ha; roots, 30 kg N/ha). The yearly amount of atmo-

spheric nitrogen fixed by rhizospheric bacteria was estimated at ~10 kg N/ha (Balandreau 1976).

Annual fires occur in January and burn the remainder of the living shoots at that time, resulting in an annual loss of ~10 kg N/ha of nitrogen from living shoots (Abbadie 1984). In the model, we assumed that the amount of remaining living shoot nitrogen in January, and hence of burned living shoots, is proportional to the maximum total grass nitrogen stock.

Litter nitrogen stock was defined at its seasonal maximum, just before annual fire, whereupon the entire stock is lost. We used a stock of 13.5 kg N/ha, which balances nitrogen inputs and outputs in the ecosystem. This amount is consistent with those found in the literature. Abbadie (1984) found 15 kg N/ha, César (1971) found 3000 kg/ha and Lavelle and Shaefer (1974) found 4000-8000 kg/ha. Assuming a nitrogen content of 0.33% of dry matter (Abbadie 1984), these estimates give a range of 10-25 kg N/ha.

Litter is decomposed both by litter-consuming fauna and by microorganisms. Data were insufficient to differentiate the direct action of fauna from that of microorganisms. However, it is likely that microorganisms perform most mineralization. Litter-consuming animals such as anecic earthworms and fungus-growing termites are regarded as litter buriers and soil bacteria and fungi activators. This role is taken into account in the parameter of litter nitrogen decomposition by microorganisms,  $d_1$ . The total flux of decomposed litter nitrogen was calculated from the monthly amount of litter biomass and nitrogen stock measured by César (1971) and Abbadie (1984) and an estimate of daily decomposition given by Le Roux (1995). An approximate flux of 20 kg N·ha<sup>-1</sup>·yr<sup>-1</sup> was thus estimated.

At equilibrium, root production equals root death. Root production was estimated as 10 000-14 000 kg·ha<sup>-1</sup>·yr<sup>-1</sup> (Menaut and César 1979). With a rough nitrogen content of 0.3% of dry weight (Abbadie 1984), these figures correspond to a nitrogen yield of 40-60 kg N·ha<sup>-1</sup>·yr<sup>-1</sup>. This range agrees with other figures from the literature (César 1971, Abbadie 1984). A mean flux of 50 kg N·ha<sup>-1</sup>·yr<sup>-1</sup> was used. Living and dead roots were not differentiated in field measurements.

As root decay in the soil occurs rapidly (Abbadie et al. 1992), we assumed that dead roots could be omitted from the model. Roughly 10% of dead roots are humified.

Rainfall supplies large amounts of organic nitrogen, 14.5 kg N·ha<sup>-1</sup>·yr<sup>-1</sup> according to Villecourt and Roose (1978). No information about the form of this organic nitrogen is available. Two alternatives seem possible. Nitrogen could be in highly humified particles adsorbed on silts transported by wind erosion. Nitrogen in this humified form, which is unlikely to be decomposed by microorganisms, should be put in the model as an input to the humic nitrogen stock compartment. Alternatively, organic nitrogen brought by rainfall could be in small, volatile organic molecules, easily decomposed by microorganisms. In this case, it should be put in the model as an input to the microorganism compartment. The former possibility was chosen, however, because it permitted us to balance the input and output of the humic stock compartment with decomposition rates by the earthworms following values given by Martin (1990). This choice has no effect on the results obtained, however. The humic nitrogen stock was estimated at 2500 kg N/ha (Abbadie 1990).

Microorganisms alone mineralize little nitrogen from the humic stock: only ~5 kg N·ha<sup>-1</sup>·yr<sup>-1</sup> (De Rham 1973). Earthworms also decompose soil organic matter. Their major effect is probably a "priming effect": they activate soil microflora. According to Martin's (1990) model, the population of *Millsonia anomala* earthworm mineralizes 5–40 kg N·ha<sup>-1</sup>·yr<sup>-1</sup>, of which only 10–50% is mineralized directly by earthworms, the remaining being mineralized by microorganisms in earthworm casts and through corpse decomposition. Their role is taken into account in the parameter of humic stock decomposition by microorganisms,  $d_0$ . A total amount of 19.5 kg N·ha<sup>-1</sup>·yr<sup>-1</sup> for decomposition of the humic stock by microorganisms was chosen to balance the humic stock compartment, which is in agreement with figures for direct decomposition by microorganisms plus earthworm mineralization and activation.

Leaching experiments carried out in lysimeters in Lamto showed that a large amount of nitrogen (5.2 kg N·ha<sup>-1</sup>·yr<sup>-1</sup>) is removed in organic form (Villecourt and Roose 1978). We assumed that this organic matter comes from products of mi-

croorganism external digestion, which gives small molecules that are easily leached.

The amount of nitrogen present in microorganisms was estimated in two different ways. First, Pochon and Bacvarov (1973) estimated  $30 \times 10^6$  bacteria/g dry soil. With a volume of 1  $\mu\text{m}^3$ /bacterium (Stolp 1988), a density of 1 g/cm<sup>3</sup>, 30% dry matter, and a nitrogen content of 14% (Stolp 1988), this amounts to 1.3  $\mu\text{g}$  N/g dry soil. We assumed that the bacteria have the same distribution in the soil as does the organic matter (Nacro 1997). The soil of Lamto contains 500  $\mu\text{g}$  N/g dry soil (Abbadie 1983), which amounts to 2500 kg N/ha. Thus, 1.3  $\mu\text{g}$  N/g dry soil amounts to 6.3 kg N/ha of bacteria in the soil. Fungi often contribute the main part of mineralization, although they usually represent a much smaller biomass and density (Kjøller and Struwe 1994). At Lamto, soil fungal biomass has not been measured. Assuming that fungi represent the same biomass as bacteria, but with a higher C/N ratio of 15–20, we obtained a biomass of 2.6 kg N/ha for soil fungi, i.e., 9 kg N/ha for microorganisms. A second estimate was calculated from the assumption that 0.5% of the carbon present in the soil is part of the bacterial and fungal biomass. Lamto soils contain 4300 g C/m<sup>2</sup> (Lavelle 1978), which gives an estimate of 15 kg N/ha of bacteria, and 7 kg N/ha of fungi. An amount of 20 kg N/ha was finally taken for this compartment.

No measure of soil mineral nitrogen content was available. The soil of Lamto is characterized by intense leaching: rainfall is high, and the soil is sandy. However, little mineral nitrogen (0.3 kg N·ha<sup>-1</sup>·yr<sup>-1</sup>) is leached (Villecourt and Roose 1978). The small amount of mineral nitrogen leached indicates that soil mineral nitrogen turnover must occur rapidly. We chose a value of 2 kg N/ha of soil mineral nitrogen, which corresponds to a residence time of 9 d (0.024 yr). These orders of magnitude seemed realistic for this compartment. Rainfall brings an input of mineral nitrogen of 4.5 kg N·ha<sup>-1</sup>·yr<sup>-1</sup> (Villecourt 1975).

The remaining fluxes were calculated in such a way as to balance inputs and outputs of each compartment: thus microorganisms mineralize 79.3 kg N·ha<sup>-1</sup>·yr<sup>-1</sup>, grass absorbs 83.5 kg N·ha<sup>-1</sup>·yr<sup>-1</sup> of soil mineral nitrogen, and 33.5 kg N·ha<sup>-1</sup>·yr<sup>-1</sup> of shoots go to the litter each year.