GRAZING OPTIMIZATION AND NUTRIENT CYCLING: WHEN DO HERBIVORES ENHANCE PLANT PRODUCTION?

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Abstract. In a general theoretical ecosystem model, we investigate the conditions under which herbivores increase primary production and lead to grazing optimization through recycling of a limiting nutrient.

Analytical and simulation studies of the model lead to several general results. Grazing optimization requires that (1) the proportion of nutrient lost along the herbivore pathway be sufficiently smaller than the proportion of nutrient lost throughout the rest of the ecosystem; and that (2) inputs of nutrient into the system be greater than a threshold value, which depends on the sensitivity of plant uptake rate to an increase in soil mineral nutrient.

An increase in nutrient turnover rate is not sufficient to explain grazing optimization in the long term. When a nutrient is the single limiting factor, plant biomass and productivity at equilibrium are determined only by the balance of ecosystem inputs and outputs of nutrient. Processes that do not have an impact on these inputs or outputs have no effect on primary producers.

On the other hand, turnover rates are important for the transient dynamics of the system, and the equilibrium analysis is relevant only if it can be reached in a reasonable time scale. The equilibrium is not reached by a compartment with a very slow turnover rate, such as the resistant soil organic matter, before several centuries. On a small time scale, such a compartment can be considered constant, and the trend of the system is predicted with a simplified system.

The results at equilibrium are insensitive to the functional form used to describe herbivore consumption: the results obtained for simple, linear, donor-controlled herbivory also apply to most forms of more realistic, recipient-controlled herbivory.

We conclude that grazing optimization is most likely to occur in systems with large losses of the limiting nutrient during recycling of plant detritus, or where herbivores bring nutrient from outside the ecosystem considered (which acts to reduce, or even make negative, the fraction of nutrient lost along the herbivore detritus pathway).

Key words: detritus pathway; grazing optimization; herbivory; input–output balance; nutrient cycling; primary production; turnover rate.

INTRODUCTION

Traditionally in ecology, plant–herbivore interactions have been considered antagonistic, i.e., herbivores have a negative effect on plants. This assumption has been questioned for some years. Indeed, many authors have suggested that herbivory can have a positive effect on plants and their productivity (Dyer 1975, Dyer and Bokhari 1976, McNaughton 1976, 1979, 1983, Owen and Wiegert 1976, 1981, Stenseth 1978, Hilbert et al. 1981, Dyer et al. 1986, Paige and Whitham 1987). This body of work has resulted in the so-called "grazing optimization hypothesis," which states that primary productivity or plant fitness at first increases with grazing and reaches a maximum at a moderate rate of herbivory (McNaughton 1979, Hilbert et al. 1981, Dyer et al. 1986).

Several mechanisms have been put forward to ac-

count for such a beneficial effect, including (1) ecological mechanisms, such as nutrient cycling; and (2) physiological mechanisms, such as plant growth promotion due to increased light intensities reaching more active underlying tissues, or to hormonal redistribution. The experimental evidence for this hypothesis has been criticized (Belsky 1986), sparking a controversy that has lasted for a decade (McNaughton 1986, Belsky 1987, Westoby 1989, Belsky et al. 1993, Dyer et al. 1993, Milchunas and Lauenroth 1993, Bergelson et al. 1996). Should the traditional view of antagonistic plants and herbivores be changed, can they even be mutualists, and under what conditions? These relationships can have important consequences for the functioning of ecosystems and plant–herbivore evolution.

Several models have been used to show that nutrient cycling by herbivores is a plausible theoretical explanation for grazing optimization of plant primary production. Simulation models show that it is theoretically possible for specific systems, such as a grassland grazed by prairie dogs (Holland et al. 1992), a lacus-
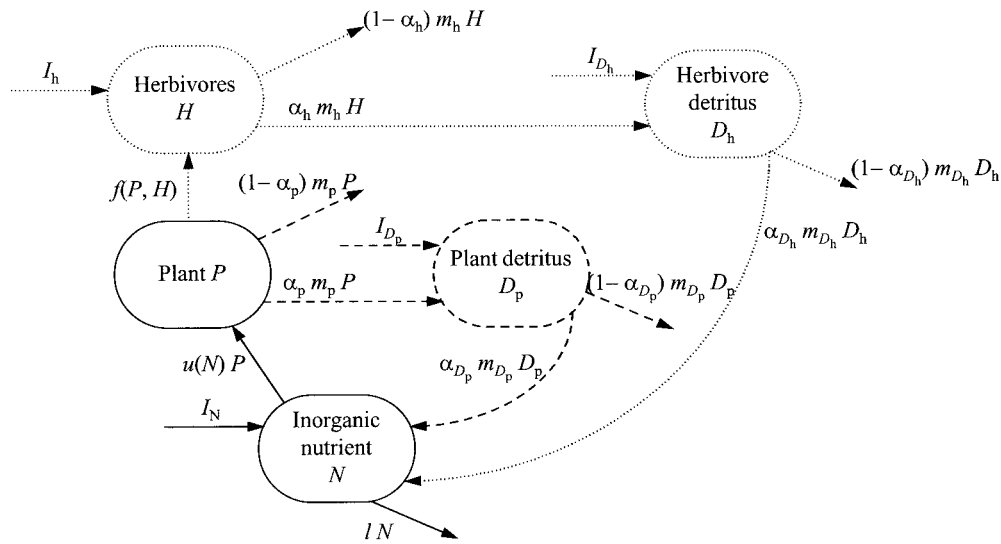
FIG. 1. Model of the cycle of a limiting nutrient in an ecosystem. A unit of the nutrient in the plant can follow either the plant detritus pathway (dashed arrows), or the herbivore pathway (dotted arrows). Definitions of parameters are found in Table 1.

trine system (Carpenter and Kitchell 1984), or a simple plant–herbivore system (Dyer et al. 1986). However, these models do not allow the analysis of necessary conditions and critical assumptions needed to obtain grazing optimization. Using a general model, De-Angelis (1992) concluded that the combinations of parameter values required to cause primary production to increase with grazing intensity are unusual. This conclusion, however, was based on an incomplete analysis of the parameter space. Loreau (1995) thoroughly analyzed these conditions in another model and reached the opposite conclusion, i.e., that grazing optimization is likely in stable, natural ecosystems. According to Loreau's model, grazing optimization occurs if herbivores sufficiently increase the ecosystem's nutrient turnover rate and if the total amount of nutrient in the ecosystem is sufficiently high.

In the present work, we develop a generalized nutrient cycle model that is simple enough to permit mathematical analysis. It leads to conditions for grazing optimization that are much more general than Loreau's (1995). We show that the effect of herbivores on plant productivity hinges, first, on the fraction of nutrient lost along the various recycling pathways rather than on the nutrient turnover rate along these pathways; and, second, on the amount of nutrient inputs into the ecosystem and the strength of plant nutrient limitation.

THE MODEL

Our compartment model of an ecosystem is as simple as possible (Fig. 1), to keep it mathematically tractable (Loreau 1995). The model differs from Loreau's (1995) in that it allows different inputs and outputs from the various compartments. All stocks and fluxes are expressed in units of the limiting nutrient. They may be

thought of as representing annual averages for the limiting nutrient, in which case the model is an average annual description of an ecosystem.

Plants absorb nutrient from a pool of inorganic nutrient (Fig. 1), which is assumed to constrain primary production. Plant nutrient can be recycled through two different pathways, termed the "plant pathway" and the "herbivore pathway." The former represents the fate of nutrient that is not consumed by the herbivore: plant dead matter either supplies plant detritus or is exported out of the ecosystem. Plant detritus is mineralized, but a fraction leaves the ecosystem through leaching or other processes.

Nutrient consumed by herbivores follows the herbivore pathway. Herbivores might immigrate (resulting in an input of herbivores into the system), leave the ecosystem, defecate in other places, or be removed from the system (resulting in an output of nutrient for the system). Herbivores produce detritus, which can be mineralized or leached from the system. Herbivore detritus may be decomposed partly by the same bacteria 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 nutrient into the system are assumed to be constant. They occur as inorganic nutrient or as organic nutrient, such as plant detritus, herbivore detritus, or through immigration of herbivores.

Most functions used for the fluxes are linear, except for plant nutrient uptake and herbivore consumption. These functions can be found in Fig. 1. Parameter definitions and units are given in Table 1.

Plant nutrient uptake $u(N)$ is proportional to plant biomass and is a function of the soil mineral nutrient

TABLE 1. Variables and parameters of the model.

Variable or parameter	Dimension	Definition
N	kg nutrient/ha	nutrient stock in the soil mineral nutrient pool
P	kg nutrient/ha	plant biomass in terms of the limiting nutrient
D_p	kg nutrient/ha	plant detritus biomass in terms of the limiting nutrient
H	kg nutrient/ha	herbivore biomass in terms of the limiting nutrient
D_h	kg nutrient/ha	herbivore detritus biomass in terms of the limiting nutrient
I_N	kg nutrient·ha^{-1}·yr^{-1}	input of mineral nutrient into the system
I_{D_p}	kg nutrient·ha^{-1}·yr^{-1}	input of organic nutrient in the form of plant detritus
I_h	kg nutrient·ha^{-1}·yr^{-1}	input of nutrient with immigration of herbivores
I_{D_h}	kg nutrient·ha^{-1}·yr^{-1}	input of organic nutrient in the form of herbivore detritus
l	yr^{-1}	mineral nutrient leaching rate
$u(N)$	yr^{-1}	plant uptake rate of mineral nutrient
m_p	yr^{-1}	plant mortality rate
m_{D_p}	yr^{-1}	plant detritus mineralization rate
m_h	yr^{-1}	rate of herbivore detritus production
m_{D_h}	yr^{-1}	herbivore detritus mineralization rate
α_p	dimensionless	fraction of plant dead matter that stays within the system and goes to plant detritus
α_{D_p}	dimensionless	fraction of the nutrient released by plant detritus that stays within the system and goes to the mineral pool
α_h	dimensionless	fraction of the nutrient released by herbivores that stays within the system and goes to herbivore detritus
α_{D_h}	dimensionless	fraction of the nutrient released by herbivore detritus that stays within the system and goes to the mineral pool
c	yr^{-1}	rate of plant consumption by herbivores (donor-controlled herbivory)

pool, N. This function describes the effect of available nutrient on the growth rate (DeAngelis 1992). Here we do not specify this function. We only assume that it is monotonic and increasing with the available nutrient.

Herbivore consumption is represented by a consumption function $f(P, H)$. Numerous functions have been used for plant–herbivore interactions (DeAngelis 1992). We first study the case of a donor-controlled trophic function, in which the consumption function depends on the donor only, here the plant. In this case, the herbivores, however numerous, graze only a given proportion of plant biomass. We chose the simplest donor-controlled trophic function, proportional to the plant compartment:

$$f(P, H) = cP \qquad (1)$$

where c, the rate of plant consumption by herbivores, is a measure of grazing intensity.

We also study the case of a recipient-controlled trophic function, in which the consumption function is proportional to the herbivore compartment:

$$f(P, H) = \gamma g(P)H \qquad (2)$$

where γ is a parameter used to measure grazing intensity, and $g(P)$ is the herbivore functional response (see Appendix). Recipient-controlled interactions, widely used in ecology, are considered more realistic for plant–herbivore interactions (DeAngelis 1992).

The model equations read as follows:

$$\frac{dN}{dt} = I_N - lN - u(N)P + \alpha_{D_p}m_{D_p}D_p + \alpha_{D_h}m_{D_h}D_h \qquad (3)$$

$$\frac{dP}{dt} = u(N)P - m_pP - f(P, H) \qquad (4)$$

$$\frac{dD_p}{dt} = I_{D_p} + \alpha_p m_p P - m_{D_p}D_p \qquad (5)$$

$$\frac{dH}{dt} = I_h + f(P, H) - m_hH \qquad (6)$$

$$\frac{dD_h}{dt} = I_{D_h} + \alpha_h m_h H - m_{D_h}D_h. \qquad (7)$$

RESULTS

Donor-controlled herbivory, equilibrium analysis

Under donor-controlled herbivory, grazing is proportional to plant biomass (Eq. 1). We are interested in how plant biomass and production vary with grazing intensity, as measured by the parameter c, the rate of plant consumption by herbivores. The equilibrium stocks of the compartments as a function of the model

TABLE 2. Lumped variables and parameters of the models.

Variable or parameter	Dimension	Meaning	Equation
Φ	kg nutrient·ha^{-1}·yr^{-1}	primary production in terms of the limiting nutrient	$\Phi = u(N)P$
S_n	kg nutrient·ha^{-1}·yr^{-1}	net nutrient supply to the system	$S_n = I_N + \alpha_{D_p}I_{D_p} + \alpha_{D_h}I_{D_h} + \alpha_h\alpha_{D_h}I_h$
β_p	dimensionless	fraction of nutrient following the plant detritus pathway that leaves the system on its way to the mineral nutrient pool	$\beta_p = (1 - \alpha_p\alpha_{D_p})$
β_h	dimensionless	fraction of nutrient following the herbivore detritus pathway that leaves the system on its way to the mineral nutrient pool	$\beta_h = (1 - \alpha_h\alpha_{D_h})$
β_t	dimensionless	total fraction of nutrient that leaves the system on its way from the plant compartment to the mineral nutrient pool	$\beta_t = (\beta_p m_p + \beta_h c)/(m_p + c)$
N_0^*	kg nutrient/ha	soil mineral nutrient pool in the ungrazed system at equilibrium	$N_0^* = u^{-1}(m_p)$
c_{max}	yr^{-1}	grazing intensity for which plant biomass becomes zero	$c_{max} = u\left(\dfrac{S_n}{l}\right) - m_p$
ΔN_0	kg nutrient/ha	see Fig. 3	$\Delta N_0 = \dfrac{m_p}{u'(N_0^*)}$

parameters are obtained by solving the system of Eqs. 1 and 3–7 after all time derivatives are set to 0. They are noted with an asterisk sign (*):

$$N^* = u^{-1}(m_p + c) \qquad (8)$$

$$D_p^* = \frac{I_{D_p} + \alpha_p m_p P^*}{m_{D_p}} \qquad (9)$$

$$H^* = \frac{cP^* + I_h}{m_h} \qquad (10)$$

$$D_h^* = \frac{I_{D_h} + \alpha_h m_h H^*}{m_{D_h}} \qquad (11)$$

$$P^* = \frac{S_n - lN^*}{\beta_p m_p + \beta_h c}. \qquad (12)$$

Primary production at equilibrium is

$$\Phi^* = uN^*P^* = \frac{S_n - lN^*}{\beta_t}. \qquad (13)$$

In these equations, u^{-1} is the inverse function of u, the plant growth rate as a function of the amount of available nutrient; S_n is the net supply of nutrient to the system; β_p is the fraction of nutrient lost along the plant detritus pathway; β_h is the fraction of nutrient lost along the herbivore detritus pathway; and β_t is the fraction of nutrient lost along both plant and herbivore detritus pathways. These lumped parameters are defined in Table 2.

Plant biomass and production as a result of input–output balance.—The equilibrium plant biomass, as given by Eq. 12, can be interpreted as the result of the ecosystem input–output balance only. Eq. (12) can be rewritten as

$$S_n = (\beta_p m_p + \beta_h c)P^* + lN^*$$

which keeps the equilibrium balance between nutrient inputs and outputs. S_n represents the net nutrient input to the ecosystem. Losses occur through mineral nutrient leaching, lN^*. All other losses of nutrient occur as organic nutrient during decomposition, which is equal to P^* times the rate of nutrient lost during decomposition along both plant and herbivore pathways.

Without herbivores, plant persistence requires that the net nutrient supply, S_n, be greater than the amount of mineral nutrient leached:

$$S_n > lN_0^* \qquad (14)$$

where $N_0^* = u^{-1}(m_p)$ is the size of the soil mineral nutrient pool in the system without herbivores.

The equilibrium stock of soil mineral nutrient (Eq. 8) depends only on the plant parameters; it is independent of the amount of nutrient that flows into, flows out of, or is mineralized within the ecosystem. Its increase with grazing intensity is due not to an increased fraction of nutrient recycled by herbivores, as one would intuitively believe (DeAngelis 1992), but to the increased consumption of plants, which reduces their ability to deplete soil nutrient (Tilman 1988).

As grazing intensity increases, the losses through leaching of mineral nutrient eventually balance the net nutrient supply for a value of the grazing intensity that we call c_{max}:

$$c_{max} = u\left(\frac{S_n}{l}\right) - m_p. \qquad (15)$$

For this value, both equilibrium plant biomass P^* and primary production Φ^* reach zero (Eqs. 12 and 13).

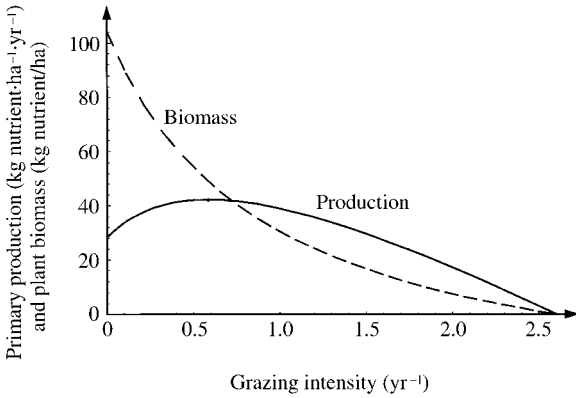Primary production can also be interpreted in terms

FIG. 2. Primary production (solid line) and plant biomass (dashed line) at equilibrium as a function of grazing intensity. A grazing optimization curve for primary production is obtained here, but plant biomass decreases with grazing intensity. Parameter values are the same as in Fig. 5b. The fraction lost along the herbivore pathway is $\beta_h = 0.1$.

of the ecosystem input–output balance only. It is equal to the net nutrient supply minus leaching losses of mineral nitrogen divided by the fraction of nutrient flowing through the plant compartment that is lost during decomposition (Eq. 13).

Nutrient cycling as a mechanism for grazing optimization.—A grazing optimization curve is obtained if and only if Φ^* increases for low values of grazing intensity (Fig. 2), i.e., if

$$\left(\frac{d\Phi^*}{dc}\right)_{c=0} > 0. \tag{16}$$

This condition becomes, after some algebraic manipulation,

$$\beta_h < \beta_p\left(1 - \frac{l\Delta N_0}{S_n - lN_0^*}\right) \tag{17}$$

where β_h and β_p represent the fractions of nutrient lost along the herbivore and plant pathway, respectively. S_n is the net nutrient supply to the ecosystem; lN_0^* corresponds to the leaching of mineral nutrient at equilibrium without herbivores; ΔN_0 is inversely proportional to the sensitivity of plant uptake rate to an increase in the soil mineral nutrient stock when the latter is at its equilibrium without herbivores (Fig. 3).

The term in brackets is <1. Thus, condition (17) says that the fraction of nutrient lost along the herbivore pathway must be sufficiently smaller than the fraction of nutrient lost along the plant pathway if herbivores are to increase primary production.

The fraction of nutrient lost along the herbivore pathway, β_h may even be negative in the case of herbivores that feed in another system and bring nutrient into the system. This seems to be the case for some fishes that feed on benthic and littoral prey and bring phosphorus to pelagic systems (Schindler et al. 1996). In such a case, condition (17) is easily fulfilled and grazing op-

timization is likely to occur. If this is not the case and herbivores do not bring nutrient into the system, the fraction of nutrient lost along the herbivore pathway, β_h, is positive. Condition (17) cannot be fulfilled if the term in brackets is negative. Thus, condition (17) can be fulfilled only if

$$S_n > lN_0^* + l\Delta N_0. \tag{18}$$

Condition (18) says that the nutrient supply to the ecosystem must be sufficient to cover leaching of mineral nutrient and a supplementary term that depends on the sensitivity of plant growth to the soil mineral nutrient stock (Fig. 3).

The full condition (17) is illustrated in Fig. 4 as a function of the net nutrient supply and the sensitivity of plant growth to an increase in soil mineral nutrient. Fig. 4a shows that once the nutrient supply, S_n, exceeds the threshold given by condition (18), the limiting fraction of losses along the herbivore pathway, as defined by (17), rapidly tends toward the fraction of losses along the plant detritus pathway. As a consequence, when the nutrient inputs in the system are sufficiently high, the condition for grazing optimization reduces to $\beta_h < \beta_p$.

To summarize, grazing optimization occurs (1) if the fraction of nutrient lost along the herbivore pathway is sufficiently smaller than the fraction of nutrient lost in the rest of the ecosystem, and (2) if nutrient inputs into the system are greater than a threshold, which decreases with the sensitivity of plant uptake rate to an increase in soil mineral nutrient. The two conditions are easily fulfilled if herbivores bring additional nutrient into the system.

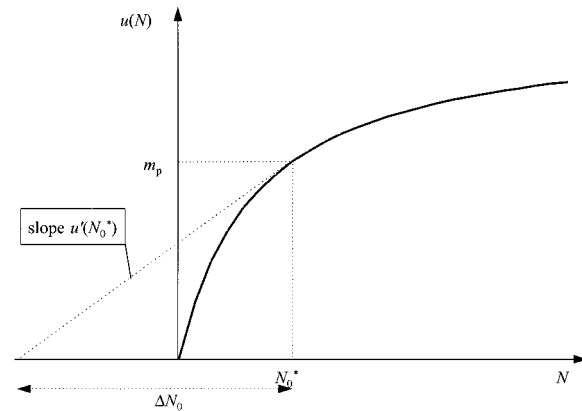Note that the equilibrium plant biomass, P^* (Eq. 12),

FIG. 3. Plant nutrient uptake rate, $u(N)$, as a function of the soil mineral nutrient pool. The slope of this curve, $u'(N)$, represents plant sensitivity to an increase in soil mineral nutrient. The parameter ΔN_0 appears in the condition of grazing optimization (Eqs. 17 and 18). $\Delta N_0 = m_p/u'(N_0^*)$ is inversely proportional to plant uptake sensitivity at the equilibrium value of the soil mineral nutrient pool without herbivores, N_0^*. Conditions for grazing optimization are more easily fulfilled if plant uptake rate is highly sensitive to an increase in soil mineral nutrient.
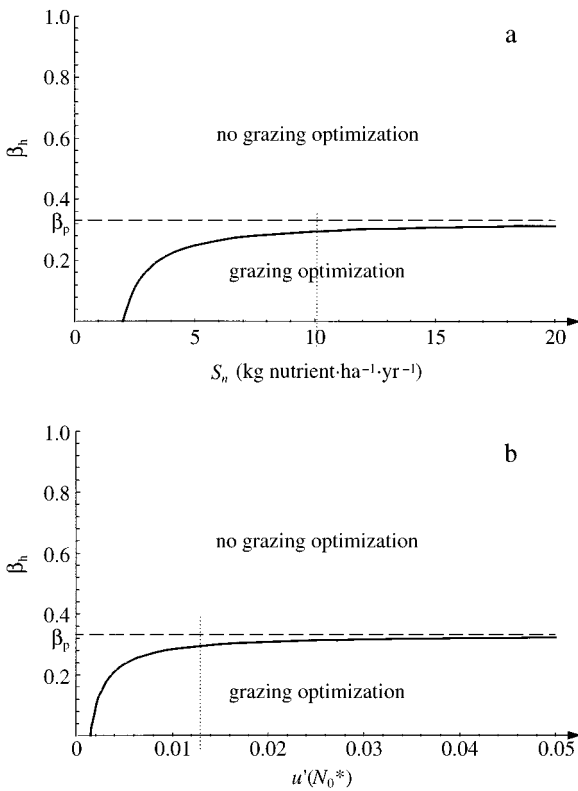
FIG. 4. Grazing optimization occurs if the fraction of nutrient lost along the herbivore pathway, β_h, is sufficiently smaller than the fraction of nutrient lost along the plant pathway, β_p (Eq. 17). This condition further requires that the net nutrient supply to the system, S_n, be sufficient (a), and that the sensitivity of plant growth rate to an increase in soil mineral nutrient, $u'(N_0^*)$, be sufficient (b). Parameter values are those for the model given in Fig. 5b ($S_n = 10.5$ kg N·ha^{-1}·yr^{-1}, $l = 0.05$/yr, $u'(N_0^*) = 0.014$, $N_0^* = 20$ kg N/ha, $m_p = 0.275$/yr, $\beta_p = 0.33$). The vertical dotted lines are (a) the net nutrient supply, and (b) the plant growth rate sensitivity for the system of Fig. 5b.

decreases with grazing intensity (Fig. 2) as long as the fraction of nutrient lost along the herbivore pathway, β_h, is positive. Even when primary production increases with grazing, the supplementary primary production is diverted towards the herbivore's profit. The equilibrium plant biomass, P^*, might increase, however, if herbivores were to introduce a new source of nutrient to the ecosystem; accordingly, the fraction of nutrient lost along herbivore pathway, β_h, would be negative.

Donor-controlled herbivory: dynamical analysis

Several authors and models (Floate 1981, Cargill and Jefferies 1984, Bazely and Jefferies 1985, Dyer et al. 1986, Ruess and McNaughton 1987, Loreau 1995) suggest that primary production depends on the rate of nutrient mineralization: the more slowly that nutrient is released by decomposition, the less nutrient is available to plants, and the less productive the ecosystem is. Nutrient turnover rates are represented by the pa-

rameters m_{D_p} for plant detritus and m_{D_h} for herbivore detritus. Their inverses, $1/m_{D_p}$ and $1/m_{D_h}$, are the mean residence times of the nutrient in the respective compartments of plant detritus and herbivore detritus. It is striking that, counter to expectations, these parameters do not even appear in the equilibrium values of plant biomass and primary production (Eqs. 12 and 13) and, hence, do not appear in the conditions for grazing optimization. In the long run, it is not the turnover rate, but the input–output balance that matters.

Although they do not affect the equilibrium state, turnover rates are major determinants of the system's dynamics. Transient dynamics are very complex and cannot be studied thoroughly in any simple way. Here, we illustrate this with a simulation study of a model of the nitrogen cycle in a grassland ecosystem (Fig. 5a), using data following Woodmansee et al. (1981).

Residence times in the different compartments are given in Fig. 5. They can be viewed as indicators of the time scales of the response to disturbance. The longest time scale is driven by the resistant soil organic matter, with 492 yr. Equilibrium analysis of the model only gives the trend of the system after several times the longest residence time, here after 2000 yr (Fig. 6a).

If we are interested in the dynamics of the model at a shorter time scale, e.g., 100 yr, we may consider that the nutrient that goes to resistant soil organic matter is lost for the system. At such a small time scale, SOM remains relatively constant and we may approximate its decomposition by a constant input. The system is then equivalent to the simplified system depicted in Fig. 5b. In this system, the longest time scale is that of plant detritus, 10 yr. The two systems have the same dynamics at <100 yr. In this case, the equilibrium analysis of the simplified model is a good approximation of the system after several times its longest time scale, ~100 yr (Fig. 6b). Dynamics of the system at a shorter time scale, such as 10 yr, depend on the turnover rates along the herbivore cycle (Fig. 6c). A study of the dynamics of the system at such a small time scale would require a much finer description of the nutrient cycle than the present model, in which recycling processes with different time scales are aggregated.

In summary, the equilibrium analysis is relevant only at a sufficiently long time scale. If we want to consider the effect of herbivores on the nutrient cycle at a time scale relevant for most ecosystem studies, i.e., several decades, the equilibrium analysis should apply to a simplified system in which resistant soil organic matter is considered constant. Turnover rates are important for the transient dynamics of the system. Herbivores may increase primary production through an increase in nutrient turnover rate, but only during transient dynamics. Such a beneficial effect may not be sustainable in the long term, the effect of herbivores on primary production being determined ultimately by the input–output balance of the system.
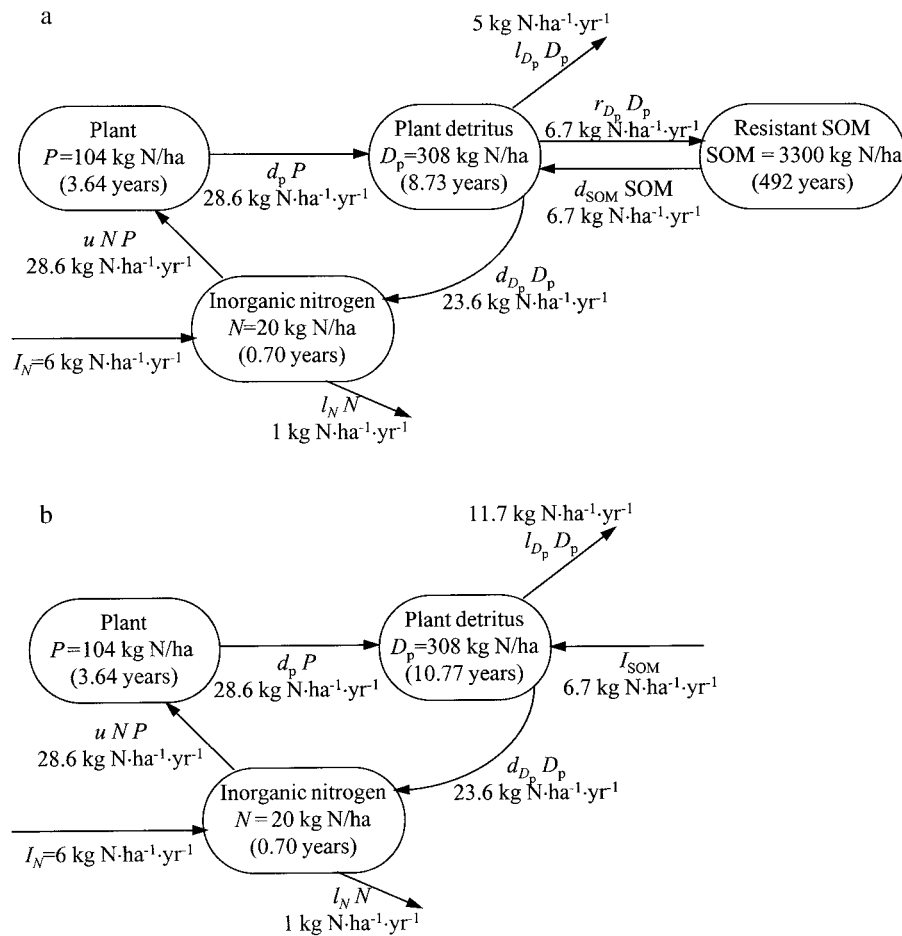
a

b

FIG. 5. (a) Model of the nitrogen cycle in a grassland ecosystem, from data after Woodmansee et al. (1981) for a short-grass prairie ecosystem. (b) Simplified model for the dynamics of the system on a ''short'' (<100-yr) time scale. Here, the resistant soil organic matter is assumed to be fixed at a constant value. Nutrient mean residence time is indicated in brackets in each compartment.

Recipient-controlled herbivory

An exhaustive study of the case of recipient-controlled herbivory (Eq. 2) is given in the Appendix. In the case of recipient-controlled herbivory, plant biomass and primary production at equilibrium are not easily interpreted from the equations (see Appendix) and do not seem to be simply the result of the input–output balance of the system.

In spite of that, the necessary and sufficient condition to obtain grazing optimization is the same as for donor-controlled herbivory (Eq. 17), and the equilibrium state of the system at the optimum productivity is identical: at the optimum, both the equilibrium values of the various compartments and the flows between them are the same. This stems from the fact that the function chosen for describing herbivore consumption has no influence on either the inputs of nutrient into the system or the fraction of nutrient lost along the herbivore pathway. Therefore, it has no influence on grazing optimization. The change in the trophic function of herbivore con-

sumption is equivalent to a change in the scale of grazing intensity. On the other hand, the form of the function does affect the transient dynamics of the system.

DISCUSSION

General theoretical conclusions

We find that the occurrence of grazing optimization through nutrient cycling relies on a simple criterion: an additional consumer should increase primary production and generate grazing optimization at equilibrium if (1) the fraction of nutrient lost along this new consumer pathway is sufficiently smaller than the fraction of nutrient lost in the rest of the ecosystem, and (2) the inputs of nutrient in the system are greater than a threshold value, which depends on the sensitivity of plant uptake rate to an increase in soil mineral nutrient.

This criterion should be tested with the knowledge of the inputs and the major sources of losses of nutrient in the ecosystem. When it is fulfilled, at equilibrium, primary production increases but plant biomass de-
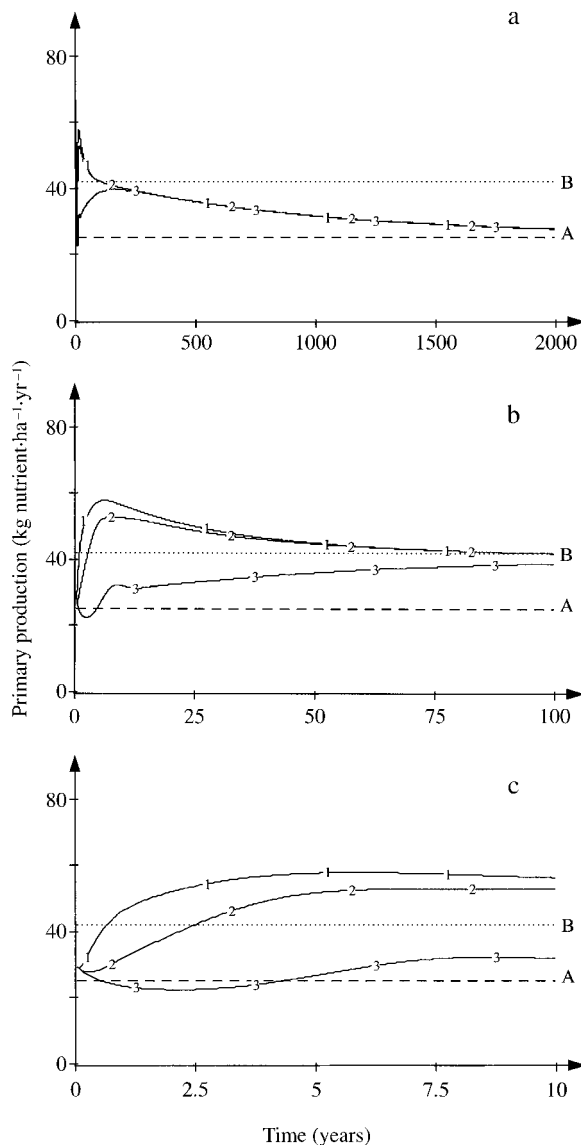
FIG. 6. Dynamics of the system in Fig. 5a, where herbivores are added (the fraction of nitrogen lost along the herbivore pathway is $\beta_h = 0.1$; grazing intensity $c = 0.5$/yr). The initial conditions are the equilibrium for the system without herbivores. At $t = 0$, grazing is introduced at a constant grazing intensity. Simulation time is 2000 yr in (a); 100 yr in (b); and 10 yr in (c). Three curves are drawn for three different residence times along the herbivore pathway: (1) 0.1 yr; (2) 1 yr; (3) 10 yr. Dashed and dotted lines, respectively, represent the equilibrium values for (A) the full system of Fig. 5a, $\Phi^* = 25$ kg N·ha^{-1}·yr^{-1}, and (B) the simplified system of Fig. 5b, $\Phi^* = 42$ kg N·ha^{-1}·yr^{-1}. The system of Fig. 5a tends to its equilibrium only after ~2000 yr. Equilibrium (B) is a good approximation of the system after 100 yr. When grazing occurs, plant biomass decreases. The plant detritus pool releases more nutrient than it absorbs, whereas herbivores first increase their biomass and thus absorb more nutrient than they release. The longer the residence time in the herbivore pathway, the longer the time required for herbivore biomass to reach a stationary value. Once the herbivore biomass reaches a sufficient value, the herbivore pathway no longer acts as a nutrient sink. Because the plant detritus pool is still above its equilibrium value, it still acts as a source of nutrient, and primary production is higher than its equilibrium value (curves 1 and 2).

creases, because all of the supplementary primary production is diverted toward the consumer's profit. Additional consumers may increase plant biomass only if they bring a new source of nutrient into the ecosystem. As a consequence, we can expect grazing optimization to be more likely in ecosystems in which large losses of the limiting nutrient occur during recycling of plant detritus. This is the case, for example, in ecosystems where fires cause large losses of nutrient (de Mazancourt et al.,*in press*).

Another prediction of the model is that herbivores are likely to have a strong, positive effect on plant production if they introduce a new source of the limiting nutrient in the system (which would result in a negative fraction of nutrient being lost along their detritus pathway). This seems to be the case in some lacustrine systems, where fishes provide an additional supply of nutrient to the pelagic system by feeding on benthic and littoral prey (Schindler et al. 1996).

Fraction of nutrient lost vs. nutrient turnover rate as a determinant of grazing optimization.—Contrary to previous suggestions (Floate 1981, Cargill and Jefferies 1984, Bazely and Jefferies 1985, Dyer et al. 1986, Ruess and McNaughton 1987, Loreau 1995), we show that, in the long term, it is not nutrient turnover rate that determines primary production, but the fraction of nutrient lost along the various cycling pathways. Apart from Loreau (1995), previous models did not take nutrient turnover rate explicitly into account, because the various detritus compartments were not represented. Loreau showed that grazing optimization requires, first, that herbivores increase the overall nutrient turnover rate and, second, that the total amount of nutrient in the ecosystem be sufficient. The model presented here leads to different and more general results, because it is based on fewer restrictive assumptions. In particular, Loreau (1995) assumed that the loss rates toward the outside world were identical for all compartments, as in a chemostat. In this case, an acceleration of nutrient circulation could only decrease the fraction of nutrient lost from a compartment. Moreover, it was the only way to decrease it. This is because an acceleration of nutrient circulation decreases the mean residence time of nutrient in a compartment and, thus, the probability that nutrient is lost from that compartment. In real systems, however, nutrient loss rates are likely to vary a great deal among compartments, as in our present model. In this case, we showed that, at equilibrium, acceleration of nutrient cycling may have no influence on primary producers if it does not result in a decrease in nutrient losses.

On a smaller time scale, an increase in nutrient turnover rate does play a role in the transient dynamics of the system, but not at equilibrium, i.e., in the long run. On the other hand, the equilibrium analysis is relevant only if it can be reached in a reasonable time scale. Turnover rates do play a role in the speed at which the equilibrium is reached. In particular, resistant soil or-

ganic matter has a very long turnover time in most terrestrial systems (Rosswall 1976). In order to evaluate an equilibrium that can be reached on an ecological time scale of decades, such resistant soil organic matter should be considered as constant.

Independence of the results from the consumption function.—As we prove in the Appendix, our results are robust to the form of interaction between plant and grazers, as long as the equilibrium is stable. Recipient-controlled herbivory is usually considered to be more realistic. Had we adopted such a function, we would not have been able to analyze the system as we did here with the simpler donor-controlled interaction, because it would have been too complicated. Therefore, it is interesting that the equilibrium state of our ecosystem model is the same, whether herbivory is a simple, linear, donor-controlled process or any form of more complex, recipient-controlled process. Changing the consumption function is then equivalent to a mere change in the scale of variation of the grazing intensity.

Limitations of the model

Our model is highly simplified and was not designed to account for all consequences of the arrival of herbivores in a system. Herbivores affect plants by trampling, by inducing physiological changes, by changing competition parameters between species, and so on (Huntly 1995). Plant regrowth after a defoliation event is unpredictable, depending on numerous factors (McNaughton 1979, Kotanen and Jefferies 1987, van der Meijden et al. 1988, Bazely and Jefferies 1989). Herbivores are known to alter the species composition of the vegetation as well (McNaughton 1985, Bazely and Jefferies 1986, Milchunas and Lauenroth 1993). These responses of vegetation to herbivory are not analyzed here, because the plants' new functional characters following herbivory cannot be predicted on the basis of present data. Therefore, the present model assumes that plant parameters are not affected by grazing.

Optimization and evolution

Our model shows that herbivores can maximize primary productivity of an ecosystem for some intermediate value of the grazing intensity. However, this does not mean that this optimal value will be reached in the evolution of plant–herbivore interactions. According to Crawley (1987), the grazing optimization controversy derives from a debate between evolutionary ecologists and ecosystem ecologists. The latter conceive that some plants may benefit from herbivory: some grasslands would not exist if herbivores did not interrupt ecological succession, and herbivores can also play a beneficial role in altering rates of nutrient cycling in an ecosystem. Conversely, evolutionary ecologists consider the fate of individual plants; for them, being consumed can only be a bad thing, and they find it hard to imagine how a strategy attracting herbivores could

be selected. Belsky et al. (1993) argue that plants always have an interest in developing a defense strategy.

In general, we argue that the grazing intensity parameter can be assumed to derive from the coevolution of plants and herbivores. Is there a potential mechanism leading to the evolution of plant–herbivore systems in such a way that primary production and, thus, energy flow in the ecosystem would be maximized? That issue should be investigated using an appropriate model that takes into account different potential levels of selection (Wilson 1976, 1980). We need more work on this aspect of coevolution between plants and herbivores before the debate can be closed.

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APPENDIX

In this Appendix, we show how the equilibrium for a system with recipient-controlled herbivory (Eq. 2) is obtained from a system with a simple, linear, donor-controlled herbivory (Eq. 1). We prove that the results obtained at equilibrium with a linear, donor-controlled herbivory can be generalized to any form of recipient-controlled herbivory.

Recipient-controlled herbivory may be written as

$$f(P, H) = \gamma g(P)H \tag{A.1}$$

where parameter γ represents a maximum rate of plant consumption per unit herbivore and will be used as a measure of grazing intensity; $g(P)$ is the herbivore's functional response. Classical functional responses (DeAngelis 1992) include the Holling type-1 functional response,

$$g(P) = P \tag{A.2}$$

as well as the Holling type-2 functional response, or Monod function,

$$g(P) = \frac{P}{K + P} \tag{A.3}$$

and the Holling type-3 or ''sigmoidal'' response,

$$g(P) = \frac{P^2}{K^2 + P^2} \tag{A.4}$$

where K is the half-saturation constant.

First, we investigate the case in which plant nutrient uptake has the form of a Lotka-Volterra interaction

$$u(N)P = uNP$$

and herbivore immigration is zero: $I_h = 0$. Solving Eqs. 3–7 at equilibrium gives

$$P^* = g^{-1}\left(\frac{m_h}{\gamma}\right) \tag{A.5}$$

$$D_p^* = \frac{I_{D_p} + \alpha_p m_p P^*}{m_{D_p}} \tag{A.6}$$

$$D_h^* = \frac{I_{D_h} + \alpha_h m_h H^*}{m_{D_h}} \tag{A.7}$$

$$N^* = \frac{m_p}{u} + \frac{m_h}{u}\frac{H^*}{G^*} = N_0^* + \frac{m_h}{u}\frac{H^*}{G^*} \qquad (A.8)$$

$$H^* = \frac{S_n - lN_0^* - \beta_p m_p P^*}{\dfrac{l}{u}\dfrac{m_h}{P^*} + \beta_h m_h} \qquad (A.9)$$

$$\Phi^* = m_p P^* + m_h H^* \qquad (A.10)$$

where g^{-1} is the inverse function of g, and remaining parameters are defined in Tables 1 and 2.

These equilibrium values are biologically feasible only for γ greater than a minimum value, γ_{min}. Herbivores must be sufficiently efficient to deplete their resource and have a positive biomass ($H^* > 0$ in Eq. A.9). The minimum value γ_{min} is that for which the herbivore population cannot be sustained, and the equilibrium is $H^* = 0$ in Eq. A.9:

$$\gamma_{min} = \frac{m_h}{g\left(\dfrac{S_n - lN_0^*}{\beta_p m_p}\right)}. \qquad (A.11)$$

In the case of recipient-controlled herbivory, we see that plant biomass at equilibrium is controlled by the herbivore parameters (Eq. A.5). It is then independent of the nutrient input–output balance of the ecosystem. Primary production (Eq. A.10) is not easily interpreted from the equations.

However, it is possible to prove formally that changing the consumption function is equivalent to simply changing the scale of grazing intensity, where parameter c is replaced by a function $h(\gamma)$, which is a function of $P^*(\gamma)$. We will show that P^* decreases with γ, and h varies between 0 and c_{max}. Then $h(\gamma)$ represents the rate of plant consumption and is constrained by the balance between nutrient inputs and outputs. Thus, in a recipient-controlled interaction, the rate of consumption $h(\gamma)$ is constrained by the input–output balance, given a certain plant biomass $P^*(\gamma)$, whereas in a donor-controlled interaction, plant biomass at equilibrium P^* (Eq. 12) is constrained by the input–output balance for a given rate of consumption c. The function chosen to describe herbivore consumption has no influence on either nutrient inputs or the percentage of nutrient lost along each pathway. Therefore, the equilibrium state of the ecosystem describes the same states in the case of a recipient-controlled herbivory when γ varies in the interval $[\gamma_{min}, +\infty]$, as in the case of the donor-controlled herbivory when c varies in the interval $[0, c_{max}]$. Hence, the optimum values for recipient-controlled herbivory are the same as those for donor-controlled herbivory. The results obtained for a simple, linear, donor-controlled herbivory can be generalized to any recipient-controlled herbivory, as long as the equilibrium is stable in the latter case.

We prove this for the general case of any continuous, monotonic, increasing functional response, such that $g(0) = 0$, and the derivative of g exists and is strictly positive. Classical functional responses (Eqs. A.2–A.4) all satisfy these conditions.

From Eqs. 1 and 2, we see that the equations for the system with recipient-controlled herbivory at equilibrium can be obtained from the corresponding equations for the system with donor-controlled herbivory by replacing c in the latter with

$$h(\gamma) = \gamma\frac{g[P^*(\gamma)]}{P^*(\gamma)}H^*(\gamma) = m_h\frac{H^*(\gamma)}{P^*(\gamma)}. \qquad (A.12)$$

This can be written as long as $P^*(\gamma)$ is different from zero, which is true for every value of γ in the domain $[\gamma_{min}, +\infty]$, as we will see.

Substituting Eq. A.9 into Eq. A.12, we have

$$h(\gamma) = \frac{S_n - lN_0^* - \beta_p m_p P^*(\gamma)}{\dfrac{l}{u} + \beta_h P^*(\gamma)}. \qquad (A.13)$$

To help understand this function, let us first investigate the equilibrium plant biomass P^* as a function of γ (Eq. A.5).

The inverse function of g, g^{-1}, is defined, continuous, and increasing (Arnaudiès and Fraysse 1989). When γ varies in the domain $[\gamma_{min}, +\infty]$, $P^*(\gamma)$ (Eq. A.5) is continuous and monotonic.

According to Eqs. A.9 and A.11, we have

$$P^*(\gamma_{min}) = g^{-1}\left(\frac{m_h}{\gamma_{min}}\right) = \frac{S_n - lN_0^*}{\beta_p m_p}. \qquad (A.14)$$

Substituting into Eq A.13, we obtain

$$h(\gamma_{min}) = 0. \qquad (A.15)$$

Assuming $g(0) = 0$, we have

$$\lim_{\gamma \to +\infty}[P^*(\gamma)] = \lim_{\gamma \to +\infty}g^{-1}\left(\frac{m_h}{\gamma}\right) = 0. \qquad (A.16)$$

Substituting into Eq. A.13 yields

$$\lim_{\gamma \to +\infty}[h(\gamma)] = \frac{u}{l}S_n - m_p \qquad (A.17)$$

where we recognize the lumped parameter c_{max} (Eq. 15 and Table 2). Thus,

$$\lim_{\gamma \to +\infty}[h(\gamma)] = c_{max}. \qquad (A.18)$$

Further, let $\Phi_1^*(c)$ be the primary productivity as a function of c in the case of donor-controlled herbivory, and $\Phi_2^*(\gamma)$ be the primary productivity as a function of γ in the case of recipient-controlled herbivory. Because the equations for the system in the first case can be obtained from the corresponding equations for the second case by replacing c in the latter with $h(\gamma)$, we have

$$\Phi_2^*(\gamma) = \Phi_1^*[h(\gamma)]. \qquad (A.19)$$

Therefore, $\Phi_2^*(\gamma)$ varies in the range $[\gamma_{min}, +\infty]$ in the same way as $\Phi_1^*(c)$ varies in the range $[0, c_{max}]$. This implies that their optimum values exist under the same conditions and, hence, are the same for donor- and recipient-controlled herbivory.

A similar proof can be done for the case in which plant nutrient uptake again has a Lotka-Volterra form, herbivore immigration I_h is not zero, and the plant–herbivore interaction has a Lotka-Volterra form ($f(P, H) = \gamma PH$).

Simulation studies showed that the same conclusion is obtained for different combinations of plant nutrient uptake (Monod or Holling type-3 growth), herbivore immigration, and herbivore functional response (Eqs. A.2–A.4).