

Effect of Herbivory and Plant Species Replacement on Primary Production

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ABSTRACT: Grazing optimization occurs when herbivory increases primary production at low grazing intensities. In the case of simple plant-herbivore interactions, such an effect can result from recycling of a limiting nutrient. However, in more complex cases, herbivory can also lead to species replacement in plant communities, which in turn alters how primary production is affected by herbivory. Here we explore this issue using a model of a limiting nutrient cycle in an ecosystem with two plant species. We show that two major plant traits determine primary production at equilibrium: plant recycling efficiency (i.e., the fraction of the plant nutrient stock that stays within the ecosystem until it is returned to the nutrient pool in mineral form) and plant ability to deplete the soil mineral nutrient pool through consumption of this resource. In cases where sufficient time has occurred, grazing optimization requires that herbivory improve nutrient conservation in the system sufficiently. This condition sets a minimum threshold for herbivore nutrient recycling efficiency, the fraction of nutrient consumed by herbivores that is recycled within the ecosystem to the mineral nutrient pool. This threshold changes with plant community composition and herbivore preference and is, therefore, strongly affected by plant species replacement. The quantitative effects of these processes on grazing optimization are determined by both the recycling efficiencies and depletion abilities of the plant species. However, grazing optimization remains qualitatively possible even with plant species replacement.

Keywords: grazing optimization, nutrient cycling, nutrient inputs and outputs, turnover rates, primary production, boreal forests.

Can herbivores increase primary production, and under what circumstances? The “grazing optimization hypothesis” has been proposed to account for positive effects of herbivory on primary production up to a moderate grazing

intensity (McNaughton 1979; Hilbert et al. 1981; McNaughton 1983; Cargill and Jefferies 1984; Dyer et al. 1986; Patten 1993). Several mechanisms could account for a positive effect of herbivores on plant production (McNaughton 1979). One possible mechanism is the effect of herbivores on the cycle of a limiting nutrient. Some authors propose that herbivores increase nutrient turnover rates (i.e., they have an accelerating effect on nutrient cycling) and that this in turn results in an increased primary production (Floate 1981; Cargill and Jefferies 1984; Bazely and Jefferies 1985; Dyer et al. 1986; Ruess and McNaughton 1987; Tilman 1988; Holland et al. 1992; Loreau 1995; Sterner 1995). Two different factors can generate such acceleration. First, following herbivory, plants regrow with a higher tissue nutrient concentration (McNaughton 1985), and the resulting litter is faster to decompose. Second, herbivores produce detritus that is more readily decomposed. This mechanism has been studied with theoretical models (Loreau 1995; de Mazancourt et al. 1998, 1999). In earlier research (de Mazancourt et al. 1998, 1999) it was shown that the acceleration of the nutrient cycle could not account for a positive effect of herbivory on primary production in the long run. Grazing optimization requires that two conditions be fulfilled: the amount of nutrient input in the system is sufficient, and herbivores contribute to improve nutrient conservation in the system.

However, some authors have also pointed out that herbivory can lead to a change in plant species composition, which can result in decreased nutrient turnover rates. This could in turn result in a decreased primary production (Pastor and Naiman 1992; Ritchie et al. 1998). As herbivores feed selectively on plant species with nutrient-rich tissues, they induce an increased abundance of plant species with nutrient-poor or defended tissues, which are very slow to decompose. If this effect were strong enough, it could prevent any enhancement of primary production by herbivory at all. Recently, Pastor and Cohen (1997) argued that plant species replacement prevents grazing optimization, in a model applied to a boreal forest where herbivory determined the relative abundance of a palatable and an unpalatable plant species.

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These two different mechanisms through which herbivory affects nutrient cycling are not contradictory. They can act in an antagonistic way, for example, if herbivore recycling stimulates primary production whereas a less productive plant species replaces a more productive one. They can also act in a synergetic way, for example, if primary production is depressed both by the herbivores recycling only a small proportion of nutrient and by replacement of a productive plant species by a less productive one. Here we present a general model of the nutrient cycle in an ecosystem with several plant species, which permits us to quantify the relative influence of these different processes, that is, herbivore recycling and plant species replacement, on primary production.

We analyze the model at an ecosystem-level equilibrium; that is, we assume that the nutrient cycle reaches a steady state, where all the stocks and fluxes in the ecosystem stay constant through time. In such a system, nutrient turnover rates (i.e., the speed of nutrient circulation in the system) do not influence primary production anymore. Only the balance between nutrient inputs and outputs does (de Mazancourt et al. 1998). This counterintuitive result can be explained as follows. Let us consider the effect of an acceleration of litter decomposition. It increases primary production in the first place by making more nutrient available to plants. However, such an effect does not last because a faster decomposition rate depletes the litter stock. As there is less litter to decompose, the amount of mineralized nutrient decreases to the same level as before the perturbation. The system goes toward its equilibrium, whose level is determined by the total amount of nutrient in the system. This in turn depends on nutrient inputs and nutrient conservation in the system. In the long term, primary production is only determined by this balance between nutrient inputs and outputs.

This has profound implications, since an acceleration or deceleration of the nutrient cycle cannot account for a change in primary production at the ecosystem-level equilibrium, that is, in the long run. The assumption of an ecosystem-level equilibrium might seem drastic at first sight, but an equilibrium model with a careful choice of parameters can approximate a transient system (de Mazancourt et al. 1998, 1999). For example, a good approximation on a 10-yr timescale is obtained by assuming that the fraction of litter that is resistant to decomposition and requires more than a decade before it is decomposed is simply constant in the ecosystem, because it would not reach an ecosystem-level equilibrium on a 10-yr timescale. Dealing with this question thus requires addressing the question of the timescale involved in the different processes explicitly. Herbivores might have different short-term and long-term effects. Thus, the type of model we

analyze here is interesting because it points out this time-scale dependency, which was not discussed before.

Is nutrient deceleration or acceleration always associated with greater or smaller nutrient losses? The answer to this question is still far from clear. It has been suggested that plant defense against herbivores would decelerate nutrient cycle and thus decrease primary production (Grime et al. 1996). But it has also been suggested that secondary compounds such as tannins may delay or prevent too quick a microbial decomposition of plant litter and thus reduce losses through leaching and increase primary production (Zucker 1983). So long as this question of nutrient losses from the ecosystem has not been addressed, the empirical relationships between plant defense and decomposition rates cannot be used to predict the long-term effects of plant species replacement on primary production.

The model we build is new because it comprises two plant types and a herbivore. The relative abundance of the two plant types is represented by one parameter that can be made to vary freely between 0 and 1. We choose a formalism such that competitive exclusion does not occur, because many processes can enable the relative abundance of plants to vary, which would not be taken into account in a simpler model. This allows us to study “artificial” situations where the herbivore can consume plants without shifting plant species composition, then change plant species composition, and study the effects of these different processes on primary production independently.

Our model is also kept relatively simple, which enables us to interpret the results obtained and to distinguish the different factors that affect primary production and its response to both herbivory and changes in species composition. These factors are, first, plant recycling efficiency (dimensionless), that is, the fraction of the limiting nutrient contained in ungrazed plant tissues that is recycled within the ecosystem to the soil mineral nutrient pool (the fraction that is not recycled is lost from the ecosystem); second, plant depletion ability, that is, the level of the soil mineral nutrient pool that is reached at equilibrium for a plant that is not consumed by herbivores (similar to Tilman’s [1982] R^* , in $\text{kg nutrient ha}^{-1}$), which determines the loss of the limiting nutrient through leaching; and, third, herbivore recycling efficiency (dimensionless), that is, the fraction of the limiting nutrient consumed by herbivores that is recycled within the ecosystem to the soil mineral nutrient pool.

We show how the condition for grazing optimization depends on plant community composition and herbivore preference, and is affected by plant species replacement. The quantitative effects of these processes on grazing optimization are determined by both the recycling efficiencies and depletion abilities of the plant species. We also show that some degree of grazing optimization remains possible,

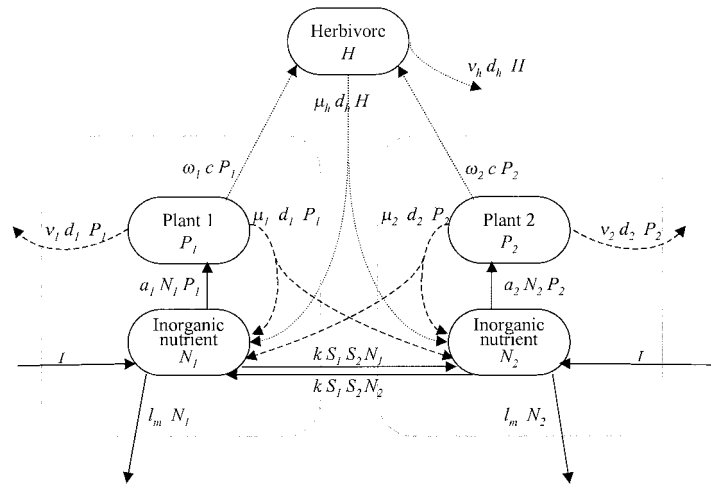


Figure 1: Model of the cycle of a limiting nutrient in an ecosystem containing two plant types, 1 and 2, with frequencies S_1 and S_2 , respectively. A unit of nutrient in a plant can follow either the plant recycling pathway (*dashed arrows*) or the herbivore recycling pathway (*dotted arrows*). Definitions of parameters are found in table 1.

provided that herbivore recycling efficiency is greater than a threshold value, even when plant species replacement occurs. Future work will be needed to fully evaluate what happens when plant traits covary. Our model suggests new field measurements and new interpretations of field data to account for the pattern of primary production with herbivory and species replacement.

The Model

The model (fig. 1) represents two plant types, 1 and 2. Plant type i occurs with relative frequency S_i , so that

$$S_1 + S_2 = 1. \quad (1)$$

Plant i 's frequency can be interpreted as the fraction of soil surface it occupies.

Each plant type absorbs nutrient locally in the inorganic nutrient pool, N_i , that is located close to its roots and is spatially segregated from the nutrient pool of the other plant type, as in Huston and DeAngelis (1994) and Loreau (1996, 1998a). Local mineral nutrient pools represent local nutrient depletion zones. Nutrient can migrate laterally in the soil between local compartments through diffusion, transport, or other processes. The amount of nutrient migrating per unit surface is assumed to be proportional to the difference in concentration between the local compartment and the mean concentration of nutrient in the soil, representing the average of a plant's neighborhood. The amount of nutrient that migrates into local pool i per unit of occupied soil surface is then $k(\bar{N} - N_i)$, where \bar{N}

is the mean amount of soil mineral nutrient per unit surface and k is the coefficient of nutrient migration in the soil.

The present model prevents competitive exclusion of different plant types, as long as the coefficient of nutrient migration in the soil is not too high (Huston and DeAngelis 1994). The frequencies of the two plant types can thus be made to vary freely.

As we explained in the opening of this article, at the ecosystem-level equilibrium, the dynamics of litter decomposition does not affect primary production. Therefore, our model assumes that plant detritus and herbivore detritus are released immediately, and their decomposition is characterized by the fraction of recycled nutrient. Our model allows for differences in nutrient recycling between the two compartments of plant detritus and herbivore detritus, as is very likely to occur (Schimel et al. 1986; Grime et al. 1996). Plant litter is assumed to be recycled in a spatially uniform way on both plant types. Another possible assumption would be that the litter of each plant is recycled locally in the local nutrient pool. The choice of one or the other assumption, however, does not affect the outcome of our model.

Herbivores graze the two plant types selectively, ω_i being their relative preference for plant type i , so that

$$\omega_1 + \omega_2 = 1. \quad (2)$$

Consumption is assumed to be proportional to plant nutrient stock and herbivore attack rate, c ; the consumption of plant i per unit of time is thus $\omega_i c P_i$. The proportion

of the standing biomass that is consumed by herbivores does not in this way depend on the density of herbivores. But our results are robust to a change in the consumption function, from a donor-controlled to a recipient-controlled Lotka-Volterra interaction, as proved in appendix A.

The dynamical equations for the various compartments thus write

$$\begin{aligned} \frac{dN_i}{dt} &= I - l_m N_i + k(\bar{N} - N_i) - a_i N_i P_i \\ &\quad + S_1 \mu_1 d_1 P_1 + S_2 \mu_2 d_2 P_2 + \mu_h d_h H, \\ \frac{dP_i}{dt} &= a_i N_i P_i - d_i P_i - \omega_i c P_i, \\ \frac{dH}{dt} &= c(S_1 \omega_1 P_1 + S_2 \omega_2 P_2) - d_h H. \end{aligned} \tag{3}$$

The dynamics of plant species replacement is represented by changes in the relative frequency of plant 1 as a function of herbivore attack rate, $S_1(c)$. The underlying assumption is that plant species replacement is slow compared with the dynamics of nutrient cycling.

Primary production is measured by the amount of the limiting nutrient taken up by the plant community per unit time. It is thus measured in terms of nutrient flow rather than biomass production. Thus, plant i 's production at equilibrium is

$$\Phi_i^* = a_i N_i^* P_i^*, \tag{4}$$

and total primary production is

$$\Phi^* = S_1 \Phi_1^* + (1 - S_1) \Phi_2^*. \tag{5}$$

All parameters are defined in table 1.

Results

General Analytical Results

Calculations and formulae are relegated to appendix B. Here, we only explain our mathematical approach and summarize the main results. The equilibrium values of the state variables, noted with an asterisk sign, are obtained by setting the time derivatives equal to 0 in (3) and solving the resulting system of equations. Primary production can thus be expressed as a function of the parameters of the model; here it will be considered a function of herbivore attack rate, c , and plant 1's frequency, S_1 .

Grazing optimization occurs if and only if primary production at equilibrium Φ^* increases with herbivore attack

rate, c , for low values of c . The variation of primary production with herbivore attack rate is

$$\frac{d\Phi^*}{dc} = \frac{\partial \Phi^*}{\partial c} + \frac{\partial \Phi^*}{\partial S_1} \frac{dS_1}{dc}. \tag{6}$$

In this equation, the first term is the variation of primary production with herbivore attack rate when no species replacement occurs, and the second term is the variation of primary production due to species replacement following herbivory. In this way, the two factors can be analyzed separately.

Identification of Two Major Plant Traits: Plant Recycling Efficiency and Plant Depletion Ability. As discussed in the above, primary production at equilibrium is only determined by the balance between the inputs and outputs of nutrient in the system. Each plant type can be characterized by the amount of nutrient lost along its own nutrient cycle (thus ignoring recycling by herbivores). Two pathways of nutrient loss along these cycles can be identified.

First, part of the nutrient is lost during recycling along the plant recycling pathway, that is, from its release by the plant to the inorganic nutrient pool. It is governed by the fraction of nutrient lost along this pathway, ν_i . We define plant i 's recycling efficiency as μ_i , where $\mu_i = 1 - \nu_i$, that is, the fraction of plant i 's dead matter that stays within the system and is recycled to the mineral nutrient pools.

Second, part of the nutrient is lost through leaching of soil mineral nutrient. The amount of nutrient lost through this process is determined by the plant's ability to deplete its available soil mineral nutrient pool. In our model, as in most other models, equilibrium results in a control of the soil mineral nutrient pool by the plant. We define plant i 's depletion ability as its capacity to depress its local nutrient pool at equilibrium without herbivores. Call this equilibrium value of plant i 's nutrient pool without herbivores R_i :

$$R_i = \frac{d_i}{a_i} = [N_i^*]_{c=0}.$$

This equilibrium value, R_i , is similar to Tilman's (1982) classical R^* , here for plant i in a system without herbivores. The lower R_i , the higher plant i 's competitive ability for the limiting nutrient in a system without herbivores.

We analyse two different cases separately: the two plant types only differ in their recycling efficiency, μ_i , and they only differ in their depletion ability, R_i . In the general case (plants differ in both their recycling efficiency and depletion ability), the various factors interact.

No Species Replacement. When there is no species replace-

Table 1: Variables and parameters of the model

	Dimension	Definition
Variable:		
N_i	kg nutrient ha ⁻¹	Amount of nutrient per unit surface in the local soil mineral nutrient pool of plant i
P_i	kg nutrient ha ⁻¹	Nutrient stock in plant i 's biomass
H	kg nutrient ha ⁻¹	Nutrient stock in herbivore biomass
Φ	kg nutrient ha ⁻¹ yr ⁻¹	Total primary production in terms of the limiting nutrient $\Phi = S_1 a_1 N_1 P_1 + S_2 a_2 N_2 P_2$
Parameter:		
I	kg nutrient ha ⁻¹ yr ⁻¹	Input of mineral nutrient into the system
l_m	yr ⁻¹	Mineral nutrient leaching rate
k	yr ⁻¹	Coefficient of migration of mineral nutrient in the soil
a_i	ha (kg nutrient) ⁻¹ yr ⁻¹	Mineral nutrient uptake rate of plant i
d_i	yr ⁻¹	Detritus production rate of plant i
d_h	yr ⁻¹	Herbivore detritus production rate
μ_i	Dimensionless	Recycling efficiency of plant i : fraction of nutrient in plant i 's dead matter that stays within the system and is recycled to the mineral nutrient pools
μ_h	Dimensionless	Recycling efficiency of herbivore: fraction of nutrient consumed by herbivores that stays within the system and is recycled to the mineral nutrient pools
ν_i	Dimensionless	Fraction of nutrient in plant i 's dead matter that leaves the system before reaching the mineral nutrient pool: $\nu_i = 1 - \mu_i$
ν_h	Dimensionless	Fraction of nutrient in herbivore detritus that leaves the system before reaching the mineral nutrient pool: $\nu_h = 1 - \mu_h$
c	yr ⁻¹	Herbivore attack rate
ω_i	Dimensionless	Herbivore preference for plant i : $\omega_1 + \omega_2 = 1$
Lumped parameter:		
R_i	kg nutrient ha ⁻¹	Plant i 's nutrient pool at equilibrium without herbivores, an inverse measure of plant i 's ability to deplete soil mineral nutrient: $R_i = d_i/a_i = [N_i^*]_{c=0}$
ν_{h+}	Dimensionless	Threshold fraction of nutrient lost along the herbivore pathway below which grazing optimization occurs, when both plant types are grazed
ν_{hi}	Dimensionless	Threshold fraction of nutrient lost along the herbivore pathway below which grazing optimization occurs, when only plant i is grazed

ment, the condition for grazing optimization is determined by the partial derivative of primary production with respect to herbivore attack rate (eq. [6]). Grazing optimization then occurs if the fraction of nutrient lost along the herbivore recycling pathway (i.e., from its release by herbivores to the inorganic nutrient pool) is smaller than a threshold value that we call ν_{h+} (app. B).

We address two questions: What is the effect of species composition on the occurrence of grazing optimization? And what is the effect of herbivore preference on the occurrence of grazing optimization? The results are summarized in table 2. The grazing optimization condition depends on the traits of the two plant types (i.e., plant recycling efficiency and plant depletion ability), on com-

munity composition, shown in table 2 for a community composed of a grazed plant type mixed with an ungrazed plant type, and on herbivore preference. Table 2 shows that all these factors play a complex role in the grazing optimization condition. The interactions between the different factors make things even more complex.

Species Replacement. The effect of species replacement on primary production is measured by the partial derivative of primary production with respect to S_1 , plant type 1's frequency. Its effect on grazing optimization is determined by the sign of this partial derivative (eq. [6]): if primary production increases (respectively, decreases) with plant type 1 frequency, grazing optimization will be easier (re-

Table 2: Effect of plant community composition, herbivore preference, and plant species replacement on the grazing optimization condition, depending on the two major plant traits, recycling efficiency and depletion ability

	Effect of plant recycling efficiency $R_1 = R_2, \mu_1 \neq \mu_2$	Effect of plant depletion ability $R_1 \neq R_2, \mu_1 = \mu_2$
Only one species present	The plant recycles efficiently (–)	The plant depletes efficiently (+)
Effect of community composition (a grazed species mixed with an ungrazed species)	The grazed plant is mixed with a plant that is more efficient at recycling (+) The grazed plant is mixed with a plant that is less efficient at re- cycling (–)	Small k : The grazed plant is mixed with a plant that is more efficient at depleting soil mineral nutrient (+) The grazed plant is mixed with a plant that is less efficient at depleting soil mineral nutrient (–) Large k : The grazed plant is mixed with a plant that is more efficient at depleting soil mineral nutrient (–) The grazed plant is mixed with a plant that is less efficient at depleting soil mineral nutrient (+)
Effect of herbivore preference	The herbivore prefers the plant that is more efficient at recy- cling (–)	The herbivore prefers the plant that is more efficient at depleting soil mineral nutrient (+)
Effect of species replacement	The plant that is more efficient at recycling increases in fre- quency (+)	The plant that is more efficient at depleting soil mineral nutrient increases in frequency (+)

Note: The sign of the effect is indicated in parentheses: a plus sign means that the characteristic indicated in the table tends to make grazing optimization easier, a minus sign means that it tends to make grazing optimization more difficult.

spectively, more difficult) if herbivores lead to replacement of plant type 2 by plant type 1.

Effect of Plant Recycling Efficiency. The plant that is more efficient at recycling keeps more nutrient in the system and thus enhances primary production. If herbivory leads to an increased (resp. decreased) frequency of the plant that is more efficient at recycling, primary production is enhanced (resp. decreased) and the grazing optimization condition becomes much less stringent (resp. more stringent).

Effect of Plant Depletion Ability. The plant that is better able to deplete soil mineral nutrient prevents more nutrient from leaching from the system and thus enhances primary production. Grazing optimization is facilitated (resp. hindered) if herbivory results in an increased (resp. decreased) frequency of the plant that is better able to deplete soil mineral nutrient.

The Example of Boreal Forests

We apply our model to provide an alternative interpretation of the case of boreal forests studied by Pastor and Cohen (1997). Their parameters represent the nitrogen cycle, with stocks expressed in kilograms of nitrogen per hectare and a time unit of a year (J. Pastor, personal communication; see table 3). We chose parameter k , the coefficient of migration of mineral nutrient in the soil, as being equal to parameter l_m , the mineral nutrient leaching rate. Because our interpretation differs from that of Pastor and Cohen, we discuss the correspondence between our model and theirs in appendix C. Plant 1 represents a tree species such as quaking aspen, which is nutrient rich, recycles better, and is preferred by herbivores. Plant 2 represents a tree species such as spruce or balsam fir, which is nutrient poor, recycles less, and is less consumed by herbivores. In boreal forests composed of these species,

Table 3: Values of model parameters that correspond to boreal forests according to Pastor and Cohen (1997)

	Value	Dimension
I	30	kg nutrient ha ⁻¹ yr ⁻¹
l_m	1	yr ⁻¹
k	1	yr ⁻¹
a_1	1.5	ha (kg nutrient) ⁻¹ yr ⁻¹
a_2	1	ha (kg nutrient) ⁻¹ yr ⁻¹
d_1	11	yr ⁻¹
d_2	10	yr ⁻¹
ν_1	$1/12 + 11/12 \times 1/2 = .5417$	Dimensionless
ν_2	$1/11 + 10/11 \times 1/2 = .5455$	Dimensionless
ω_1	$1/1.1 = .91$	Dimensionless
ω_2	$.1/1.1 = .09$	Dimensionless
R_1	$d_1/a_1 = 7.33$	kg nutrient ha ⁻¹
R_2	$d_2/a_2 = 10$	kg nutrient ha ⁻¹

the main mammalian herbivores are the moose and the snowshoe hare.

In this case, the two tree species are very similar with respect to recycling efficiency when parameters derived from Pastor and Cohen (1997) are used (table 3). Plant 1 is only slightly more efficient at recycling than plant 2. On the other hand, the two species differ much more in their depletion abilities (table 3). Plant 1 is much better at depleting soil mineral nutrient than is plant 2.

The reduction of primary production when plant 2 replaces plant 1 is mainly due to this difference in plant depletion abilities (table 4). The difference between plant recycling efficiencies only accounts for 4% of the difference in production. It is negligible compared with the reduction of primary production due to plant depletion abilities (94% of the difference). The interaction between the two effects accounts for the rest of the reduction of primary production (2%).

No Species Replacement. With these parameter values, we calculated the maximum fraction of nutrient lost along the herbivore recycling pathway that allows grazing optimization, depending on the frequencies of the two plant types (fig. 2). Grazing optimization is possible when no species replacement occurs. It requires that losses along the herbivore recycling pathway be smaller than the threshold fraction ν_{h+} , which is between 0.27 and 0.37 depending on the composition of the plant community (fig. 2). Such a low fraction was impossible in Pastor and Cohen's (1997) model because the losses along the herbivore recycling pathway were necessarily at least as high as those of the common pool of detritus, that is, 0.50. Thus, in their model, grazing optimization was impossible even for pure strands of either plant.

Species Replacement and Grazing Optimization. Grazing op-

timization is possible even with replacement of the more productive species 1 by the less productive species 2, if the fraction of nutrient lost along the herbivore recycling pathway is sufficiently low. Figure 3 shows the result of a very simple scenario of plant species replacement: plant 1 frequency, S_1 , decreases linearly with herbivore attack rate as measured by parameter c , up to a maximum attack rate c_{\max} at which plant 1 frequency reaches 0. This parameter, c_{\max} , was chosen just below the attack rate at which plant 1 biomass would reach 0.

In figure 3A, primary production and herbivore consumption are shown as a function of attack rate c . Curve 1 shows primary production in a pure strand of plant 1 as a function of attack rate. It is a grazing optimization curve, with a strong positive response to grazing intensity, followed by a rapid decrease leading to its extinction due to overgrazing. Curve 2 shows primary production when plant species replacement occurs. Primary production first increases because of a better recycling by herbivores. Then it reaches a maximum and decreases when herbivore attack rate increases. Finally, it increases again as the second plant species, which is less grazed than the first, increases in abundance. Under these circumstances, species replacement can be seen as a process that enables the system to maintain a high productivity under a high grazing pressure. Herbivore consumption when plant species replacement occurs (curve 5) follows a similar pattern. It decreases at a high attack rate because of two processes. First, overgrazing of the first species leads to a decrease of primary production and thus of the amount of available food. This can be seen in the corresponding decrease in curve 4, herbivore consumption in a pure strand of plant 1. Second, species replacement leads to dominance of the less consumed species. This second processes is reflected by the fact that herbivore consumption goes toward curve 6, herbivore consumption in a pure strand of plant 2, when plant 1 is replaced by plant 2.

Figure 3B shows the peculiar pattern of primary production that is generated as a function of another common measure of grazing intensity, the percentage of primary production consumed. This nonintuitive pattern results from the nonlinear dependency of both primary production and herbivore consumption on attack rate.

Discussion

General Theoretical Conclusions

In the long term, at an equilibrium in which all the nutrient stocks and flows have reached a steady state, primary production is determined by the balance between nutrient inputs and outputs in an ecosystem. Our model shows that under these conditions the patterns of primary pro-

Table 4: Primary production and plant species composition in boreal forests: effects of plant recycling efficiencies and plant depletion abilities

	Primary production (kg nutrient ha ⁻¹ yr ⁻¹)	Difference between plant 1 and plant 2 production (kg nutrient ha ⁻¹ yr ⁻¹)	Effect
Plant 1 alone	41.9
Plant 2 alone	36.7	5.2	...
Plant 2 with same recycling efficiency as plant 1	36.9	4.9	Effect of plant depletion ability: 94% of the difference
Plant 2 with same depletion ability as plant 1	41.6	.3	Effect of plant recycling efficiency: 4% of the difference

duction as a function of herbivory and community composition are more complex than previously recognized. They are determined by three major factors that affect nutrient outputs from the ecosystem: plant recycling efficiency, that is, the fraction of the plant nutrient stock that stays within the ecosystem until it is returned to the nutrient pool in mineral form; plant depletion ability, that is, the ability of the plant to deplete the soil mineral nutrient pool and thus to reduce losses through leaching of mineral nutrient, which is related to plant competitive ability; and herbivore recycling efficiency, that is, the fraction of the nutrient consumed by herbivores that is recycled within the ecosystem to the mineral nutrient pool.

Grazing optimization occurs if herbivores recycle the nutrient within the system sufficiently. It depends on plant community composition, herbivore preference, and plant species replacement. The effects of these processes on grazing optimization conditions (summarized in table 2) are complex, and depend on both the recycling efficiencies and depletion abilities of the plant species. But grazing optimization remains possible even in the worst case, when herbivores prefer the plant that is more efficient at recycling, and lead to species replacement toward the less efficient plant at both recycling and depleting soil mineral nutrient, provided that herbivores are sufficiently efficient at recycling nutrient.

This model was kept reasonably simple and, therefore, was not intended to answer all the questions that arise with plant species replacement. For example, we do not explore the cases where herbivory is so intense that it creates bare patches. We also address the question of plant evolution and trade-off between herbivore resistance and competitive ability in another paper (C. de Mazancourt, M. Loreau, and U. Dieckmann, in preparation).

The Case of Boreal Forests

Our model yielded unexpected interpretations when applied to boreal forests, which suggest new field measurements. We showed that grazing optimization is possible in this case, but it requires that herbivores recycling efficiency be high: it must be >0.63 or 0.73 , depending on the initial species composition. Grazing optimization could occur if more than two-thirds of nutrient consumed by herbivores are recycled and mineralized in the ecosystem.

Our interpretation differs from that of Pastor and Cohen (1997) because the plants in their model did not actually differ in their recycling efficiency but in their depletion ability. The decrease in primary production predicted by the models following species replacement was due to the fact that the losses of the limiting nutrient through leaching in mineral form increased, because the tree species that invaded the system was less efficient at depleting the soil mineral nutrient pool. This emphasizes the potential importance of plant depletion ability, which has very seldom been taken into account in previous debates, measurements and theories. Because of the constraints in Pastor and Cohen's model, the lower depletion ability of plant 2 was required in order to have coexistence of the two plants and their replacement with the herbivore: the coexistence of the two plants hinged on the herbivore preferring the most competitive species for nutrients. It would be interesting to test this assumption in the field.

Our comparison of our model with Pastor and Cohen's (1997) indicate that their conclusion that an increase of primary production was impossible with herbivory was due to the fact that herbivores did not recycle nutrient sufficiently. This result was constrained by their assump-

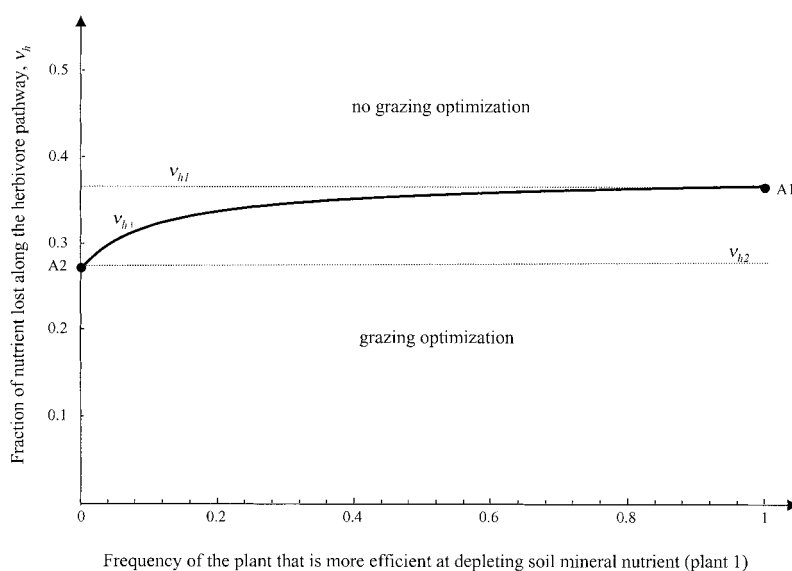


Figure 2: Threshold fraction of nutrient lost along the herbivore pathway below which grazing optimization occurs, as a function of the frequency of the plant that is more efficient at depleting soil mineral nutrient (plant 1) in the case of boreal forests as described by Pastor and Cohen (1997). $A1$ = threshold for a pure stand of the plant that is more efficient at depleting soil mineral nutrient. $A2$ = threshold for a pure stand of the plant that is less efficient at depleting soil mineral nutrient. v_{h1} = threshold when only the most efficient plant is grazed. v_{h2} = threshold when only the less efficient plant is grazed. v_{h+} = threshold when both plants are grazed. (Parameter values as in table 3: $I = 30$ kg nutrient $\text{ha}^{-1} \text{yr}^{-1}$; $l_m = 1$ yr^{-1} ; $k = 1$ yr^{-1} ; $a_1 = 1.5$ ha (kg nutrient) $^{-1} \text{yr}^{-1}$; $a_2 = 1$ ha (kg nutrient) $^{-1} \text{yr}^{-1}$; $d_1 = 11$ yr^{-1} ; $d_2 = 10$ yr^{-1} ; $v_1 = 0.5417$; $v_2 = 0.5455$; $\omega_1 = 0.91$.)

tion of a common detritus pool for all plant and herbivore detritus. In reality, such different detritus as plant and herbivore detritus are not likely to follow the same decomposition processes (Schimel et al. 1986; Grime et al. 1996).

The present model thus highlights the necessity of careful field measurements in order to check which of the proposed mechanism is at work in the field. We suggest measures of the different pathways of nutrient losses in the system, as these should drive primary production on the long term.

The Identity of Plant Species, Herbivory, and the Ecosystem Nutrient Budget

We briefly discuss possible processes of nutrient loss along the three major pathways revealed by our model. Plant species replacement due to herbivory is likely to result in significant changes in the patterns of nutrient inputs and outputs, because plant defense may control many of the processes that determine them.

Plant Recycling Efficiency. Losses of nitrogen along the plant recycling pathway can occur through various processes: volatilization from senescing tissues (Schimel et al. 1986), fire (Ojima et al. 1994; de Mazancourt et al. 1999), and

leaching of organic matter during decomposition processes. Plant defenses are likely to play a role in plant recycling efficiency. Zucker (1983) suggested that secondary compounds such as tannins, which are involved in plant antiherbivore defense, may reduce losses of nutrients such as nitrogen because it prevents the breakdown of plant litter too quickly. Monoterpenes, which are another antiherbivore defense, are highly flammable compounds (White 1994) and might increase nutrient loss by fire.

Plant Depletion Ability. Plants can affect nutrient concentrations in the soil (Tilman and Wedin 1991a, 1991b). Leaching of mineral nutrient is driven by the soil concentration of the labile form of the nutrient (NO_3^- for nitrogen). Plant species do have different effects on nutrient leaching losses depending on their functional group (Hooper and Vitousek 1998). Denitrification may also depend on nitrate depletion by root uptake among other factors (Bakken 1988).

The ability to deplete soil nutrient affects plant competitive ability for soil nutrients, and species replacement tends toward the dominance of the species that is best at depleting soil mineral nutrient (Tilman 1988; Tilman and Wedin 1991a, 1991b), thus leading to a tighter nutrient cycling in ecosystems (Loreau 1998b). Thus, plant control of soil mineral nutrient is likely to drive the amount of

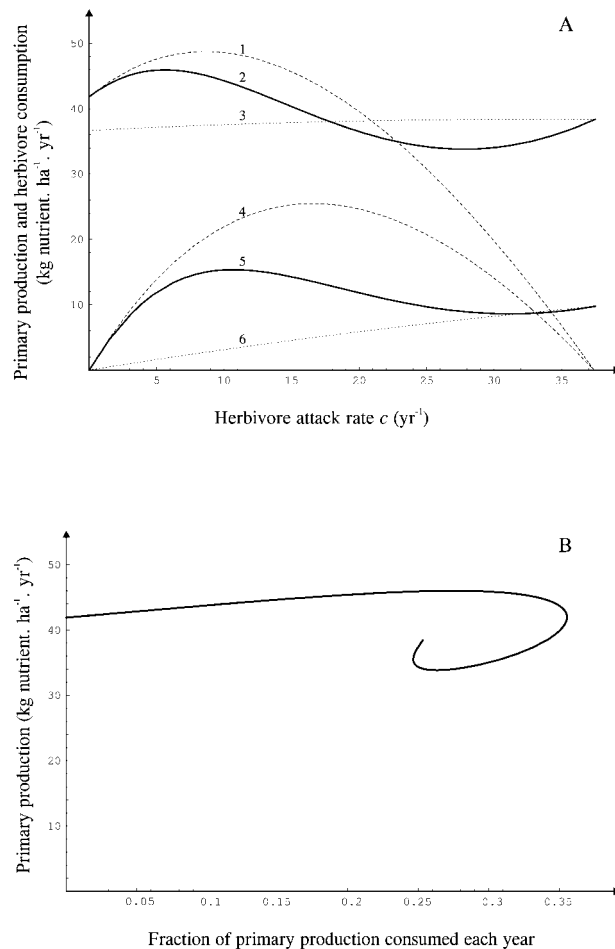


Figure 3: A, Primary production (curves 1–3) and herbivore consumption (curves 4–6) as functions of herbivore attack rate c . *Continuous lines* (curves 2 and 5): scenario of plant species replacement in the case of boreal forests (table 3) with replacement of the more productive species by the less productive species: the frequency S_1 of plant 1, the more productive species, decreases linearly with herbivore attack rate as measured by parameter c . *Dashed lines* (curves 1 and 4): no species replacement, only the most productive species, plant 1 is present. *Dotted lines* (curves 3 and 6): no species replacement, only the less productive species, plant 2 is present. B, Primary production as a function of grazing intensity as measured by the fraction of primary production consumed in the scenario of plant species replacement. (Parameter values as in fig. 2, and $S_1 = 1 - c/37.5$, $\nu_h = 0.1$.)

nutrient lost through leaching of mineral nutrient and denitrification, as in our model.

On the other hand, in some ecosystems such as grasslands, nitrates often occur in sub-ppm concentrations, so that little is susceptible to leaching and denitrification, except in urine patches (Woodmansee et al. 1981). If such is the case, the different levels of plant depletion of soil mineral nutrient may have only a negligible effect on the outputs of nitrogen through leaching and denitrification.

Other Effects of Secondary Metabolites on Nutrient Inputs and Outputs. Nutrient recycling and depletion are the two processes represented in our model by which plants affect

nutrient outputs from the ecosystem. But any other process by which plants affect inputs and outputs of the limiting nutrient will have a strong influence on primary production and grazing optimization. Plants might control denitrification rates, independently of their ability to deplete soil nitrate concentration, as is suggested by Bakken (1988). Plant secondary metabolites are likely to affect nutrient inputs and outputs in a variety of ways. White (1994) suggested that monoterpenes may affect nitrogen inputs and outputs through inhibition of nitrification, which results in a reduction of nitrogen loss by denitrification. Monoterpenes are known to favor or to inhibit different microorganisms and may either stimulate or in-

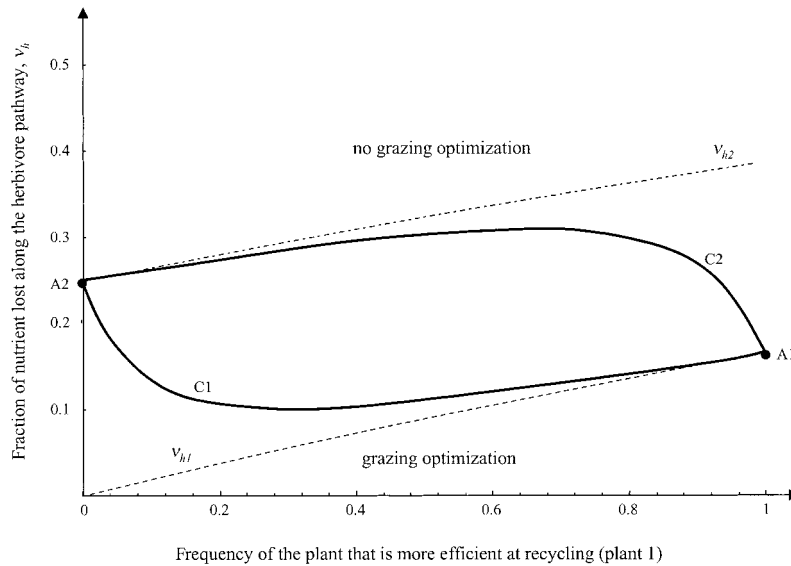


Figure 4: Threshold fraction of nutrient lost along the herbivore pathway below which grazing optimization occurs, as a function of the frequency of the plant that is more efficient at recycling (plant 1). A_1 = threshold for a pure stand of the plant that is more efficient at recycling. A_2 = threshold for a pure stand of the plant that is less efficient at recycling. v_{h1} = threshold when only the plant that is more efficient at recycling is grazed. v_{h2} = threshold when only the plant that is less efficient at recycling is grazed. C_1 = threshold when the plant that is more efficient at recycling is preferred. C_2 = threshold when the plant that is less efficient at recycling is preferred. (Parameter values: $I = 30 \text{ kg nutrient ha}^{-1} \text{ yr}^{-1}$; $l_m = 1 \text{ yr}^{-1}$; $k = 1 \text{ yr}^{-1}$; $a_1 = a_2 = 1 \text{ ha (kg nutrient)}^{-1} \text{ yr}^{-1}$; $d_1 = d_2 = 10 \text{ yr}^{-1}$; $v_1 = 0.33$; $v_2 = 0.5$; curve C1: $\omega_1 = 0.91$; curve C2: $\omega_1 = 0.09$.)

hibit nitrogen fixation. The effects of plant antiherbivore defense on nutrient inputs and outputs are thus likely to be numerous and complex.

Herbivore Recycling Efficiency. A review of herbivore recycling efficiency for nitrogen can be found in de Mazancourt et al. (1999). Several authors suggested that herbivores are a major pathway of nitrogen losses in grasslands (Denmead et al. 1974; Woodmansee et al. 1981; Ryden et al. 1984). Others concluded that herbivores contribute to nitrogen conservation (Schimel et al. 1986; Ruess and McNaughton 1988; Frank and Zhang 1997). There is still a lack of knowledge on the conditions under which herbivores are likely to recycle nutrient efficiently. Herbivores might also affect plant recycling efficiency, for example, if the reduction of plant litter leads to a nonlinear decrease in the intensity of fire.

Implications for General Theories of Herbivory and Nutrient Cycling

Two extreme cases of effects of herbivores on nutrient cycling have been distinguished, leading to the following theory as expressed by Hobbie (1992). In nutrient-poor environments, plants lack nutrient for growth but have carbon in excess. Therefore, they invest heavily in carbon-

based secondary metabolites that deter herbivores, but also slow down nutrient cycling. In such environments, herbivory results in increased abundance of plants with secondary compounds, which slow down nutrient cycling and decrease primary production. Evidence for this first point is scant and comes mainly from boreal forests (McInnes et al. 1992; Pastor and Naiman 1992; Pastor et al. 1993; Pastor and Cohen 1997). Similar effects were obtained in South African savanna-woodlands (references in Bryant et al. 1991) and in an oak savanna (Ritchie et al. 1998). In contrast, in nutrient-rich ecosystems, herbivores increase nutrient cycling rates and thus enhance nutrient availability. Herbivory results in an increase of primary production. Evidence for this second point comes mainly from the Serengeti savanna ecosystem (McNaughton et al. 1997) and La Perouse Bay ecosystem (Ruess et al. 1989). According to Bryant et al. (1991), these effects do not depend on the system being rich or poor, but on whether plants are graminoids or woody plants because the latter have more chemical defenses against mammalian herbivores.

This study suggests that interpretations based on a positive or negative effect of herbivores on nutrient turnover rates are insufficient to address long-term results, because primary production at equilibrium is only determined by the balance between nutrient inputs and outputs. We suggest a different approach, based on the nutrient budget,

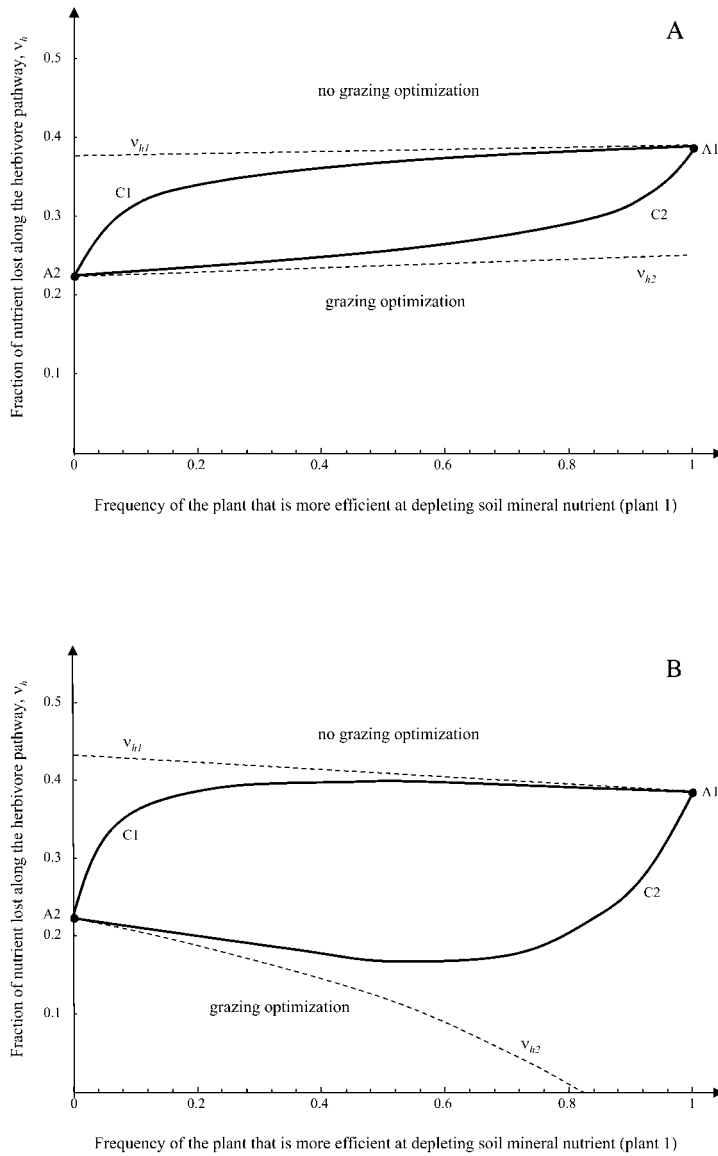


Figure 5: Threshold fraction of nutrient lost along the herbivore pathway below which grazing optimization occurs, as a function of the frequency of the plant that is more efficient at depleting soil mineral nutrient (plant 1). A, Small coefficient of migration of mineral nutrient in the soil ($k = 0 \text{ yr}^{-1}$). B, Large coefficient of migration of mineral nutrient in the soil ($k = 5 \text{ yr}^{-1}$). $A1$ = threshold for a pure stand of the plant that is more efficient at depleting soil mineral nutrient. $A2$ = threshold for a pure stand of the plant that is less efficient at depleting soil mineral nutrient. v_{h1} = threshold when only the more efficient plant is grazed. v_{h2} = threshold when only the less efficient plant is grazed. v_{h+} = threshold when both plants are grazed. (Parameter values: $I = 30 \text{ kg nutrient ha}^{-1} \text{ yr}^{-1}$; $L_m = 1 \text{ yr}^{-1}$; $a_1 = 1.5 \text{ ha (kg nutrient)}^{-1} \text{ yr}^{-1}$; $a_2 = 1 \text{ ha (kg nutrient)}^{-1} \text{ yr}^{-1}$; $d_1 = 10 \text{ yr}^{-1}$; $d_2 = 11 \text{ yr}^{-1}$; $v_1 = v_2 = 0.54$; curves C1: $\omega_1 = 0.91$; curves C2: $\omega_1 = 0.09$.)

notably to measure the different key parameters identified in this study: plant recycling efficiency, plant depletion ability and herbivore recycling efficiency. This should be more appropriate to study long-term effects. Acceleration

or deceleration of nutrient cycles may play a role on a small timescale, however (de Mazancourt et al. 1998). Consequently, the timescale considered should at least be discussed.

For example, Ojima et al. (1994) showed two effects of fire on nitrogen cycling. On a small timescale, fire enhanced microbial activity, plant above- and belowground production and plant nitrogen-use efficiency. But fire volatilized most of the nitrogen in plant litter and, on a longer timescale, reached only after 2 yr, fire resulted in a lower nitrogen availability. Thus, in the long term, the effects of fire depended on nitrogen outputs. Similar patterns for the effects of herbivore on nutrient cycling at different timescales should be searched for.

The effect of herbivory on nutrient cycling and primary production is likely to be much more complicated than a simple acceleration/deceleration effect. We argue that the effect of herbivores on nutrient inputs and outputs could be much more important for primary production.

Acknowledgments

We would like to thank M. Leibold for his constructive comments on a previous version of this manuscript.

APPENDIX A

Lotka-Volterra Herbivory

Here we present a rationale that explains why the results obtained for a Lotka-Volterra interaction, where herbivore consumption of plant i is $\omega_i \gamma P_i H$, should be the same as those obtained with a simple donor-controlled herbivory, where herbivore consumption of plant i is $\omega_i c P_i$. We do not make a formal proof here, because the equations become rapidly very complicated. A formal proof for a simpler case can be found in de Mazancourt et al. (1998). The equivalence of the two systems were checked in the case of the boreal forests discussed in the text.

The equilibrium biomass of each compartment and equilibrium fluxes between the compartments are constrained by the nutrient input–output balance. Both Lotka-Volterra and donor-controlled systems have the same constraints; therefore, for a given herbivory pressure, their equilibrium values are identical.

Let us first consider the case of a system where the relative frequency of each plant type, S_i , is fixed. The equations of the simple donor-controlled system can be obtained from the equations of the Lotka-Volterra system with a simple change of parameter:

$$c = \gamma H^*,$$

where c is the donor-controlled herbivore attack rate (yr^{-1}), γ is the Lotka–Volterra herbivore attack rate (in $\text{kg nutrient ha}^{-1} \text{yr}^{-1}$), and H^* is the equilibrium herbivore compartment (in $\text{kg of nutrient ha}^{-1}$) in the Lotka–Volterra system. With this parameter change, the equilibrium biomasses of each compartment in the two systems are determined by exactly the same equations, and hence are identical.

So long as the function γH^* is monotonic increasing with γ , the two systems (donor controlled and Lotka–Volterra) describe exactly the same successive states as their respective rates of herbivory increase. The change from one system to the other is equivalent to a mere change of the scale of the parameter measuring herbivore attack rate, because the two rates do not have the same meaning and dimension. If we choose to represent primary production as a function of the same grazing intensity measure, for example, the fraction of primary production consumed, then the two systems yield exactly the same results. This holds for the cases where no species replacement occurs.

Let us now consider the case with species replacement. In the Lotka–Volterra system, the equilibrium herbivore compartment depends on all model parameters, notably herbivore attack rate γ and plant frequencies, which we summarize in parameter S_1 (because $S_2 = 1 - S_1$):

$$H^* = H^*(\gamma, S_1).$$

Now S_1 is a function of herbivore attack rate: $S_1 = S_1(\gamma)$. The Lotka–Volterra system is equivalent to a donor-controlled system where

$$c = \gamma H^*[\gamma, S_1(\gamma)] \text{ and } S_1 = S_1(\gamma).$$

Thus, the two systems are equivalent given appropriate changes in the function of plant species replacement and herbivore attack rate.

APPENDIX B

Model Analysis

Primary production at equilibrium is obtained by solving equations (3)–(5) where all time derivatives are set to 0:

$$\Phi^* = \frac{(d_1 + \omega_1 c)(d_2 + \omega_2 c)[I - l_m(R_1 S_1 + R_2 S_2)] + S_1 S_2(l_m + k)(R_2 - R_1)[\omega_1 c d_2(\mu_h - \mu_2) + d_1 \omega_2 c(\mu_1 - \mu_h) + d_1 d_2(\mu_1 - \mu_2)]}{(d_1 + \omega_1 c)(d_2 + \omega_2 c) - (d_2 + \omega_2 c)(\omega_1 \mu_h c + \mu_1 d_1) S_1 - (d_1 + \omega_1 c)(\omega_2 \mu_h c + \mu_2 d_2) S_2},$$

where all parameters can be found in table 1.

Mathematical Approach

The results in the general case are too complicated to be interpreted in a simple way. Therefore, we only present our mathematical approach, which will then be applied in the following sections to identify and to study the separate effects of the two major plant traits, that is, plant recycling efficiency and plant depletion ability.

No Species Replacement

When there is no species replacement, the variation of primary production with herbivore attack rate is given by equation (6):

$$\frac{d\Phi^*}{dc} = \frac{\partial\Phi^*}{\partial c}.$$

Grazing optimization occurs if primary production presents a maximum for a positive value of herbivore attack rate. Equation $\partial\Phi^*/\partial c = 0$ is a second-degree equation in c , and grazing optimization occurs if and only if

$$\left[\frac{\partial\Phi^*}{\partial c} \right]_{c=0} > 0,$$

which yields a condition of the form $\nu_h < \nu_{h+}$. Grazing optimization occurs if the percentage of nutrient lost along the herbivore recycling pathway is smaller than a threshold value that we call ν_{h+} . If only plant 1 is grazed ($\omega_1 = 1$ and $\omega_2 = 0$), we call this threshold value ν_{h1} , which is found to be

$$\nu_{h1} = \frac{\alpha_1}{\beta_1},$$

where

$$\alpha_1 = \nu_1[I - l_m(S_1 R_1 + S_2 R_2)] - l_m R_1(S_1 \nu_1 + S_2 \nu_2) + (l_m + k)S_2[\nu_1 \nu_2(R_2 - R_1) - R_1(S_1 \nu_1 + S_2 \nu_2)(\nu_2 - \nu_1)],$$

$$\beta_1 = I - l_m(S_1 R_1 + S_2 R_2) - (l_m + k)\nu_2 S_2(R_1 - R_2).$$

In the same way, if only plant 2 is grazed ($\omega_1 = 0$ and $\omega_2 = 1$), we call this threshold ν_{h2} , which is identical to ν_{h1} except for the appropriate substitutions of subscripts.

When the two plant types are grazed, the threshold for grazing optimization can be expressed as a function of the α 's and β 's:

$$\nu_{h+} = \frac{\alpha_1 d_2 \omega_1 S_1 + \alpha_2 d_1 \omega_2 S_2}{\beta_1 d_2 \omega_1 S_1 + \beta_2 d_1 \omega_2 S_2}.$$

The threshold for grazing optimization in a community where the two plant types are grazed is intermediate between the two thresholds for grazing optimization when only one of either plant type is grazed.

Effect of Community Composition. The effect of community composition on the occurrence of grazing optimization is given by the derivative of the threshold ν_{h+} with respect to plant frequency: if $d\nu_{h+}/dS_1$ is positive, then the grazing optimization condition (without species replacement) is less stringent when plant 1 is more frequent in the community.

Effect of Herbivore Preference. The effect of herbivore preference on the occurrence of grazing optimization is given by the derivative of the threshold with respect to herbivore preference: if $d\nu_{h+}/d\omega_1$ is positive, then the grazing optimization condition (without species replacement) is less stringent when plant 1 is more preferred by herbivores.

Species Replacement

The effect of species replacement on grazing optimization is given by the partial derivative of primary production with respect to plant type 1 frequency (eq. [6]). If $\partial\Phi^*/\partial S_1$ is positive, then primary production increases with the frequency of plant 1. Thus, grazing optimization will be facilitated if herbivory leads to replacement of species 2 by species 1. Conversely, it will be hindered if herbivory leads to replacement of species 1 by species 2.

First, we analyze the case when the two plant types only differ in their fraction of nutrient lost along the plant recycling pathway, ν_i . Second, we analyze the case when the two plant types only differ in their depletion ability, R_i (table 1).

Effect of Plant Recycling Efficiency

Here we assume that plant types 1 and 2 have the same nutrient uptake rate and detritus production rate; that is,

$$a_1 = a_2 = a,$$

$$d_1 = d_2 = d_p,$$

and consequently, the same competitive abilities without herbivores:

$$R_1 = R_2 = R.$$

Only One Species Present

In a community with only one plant species, grazing optimization occurs if

$$\nu_h < \nu_p \frac{I - 2l_m R}{I - l_m R},$$

where ν_p is the fraction of nutrient lost along the plant recycling pathway. Thus, grazing optimization occurs if herbivores help to keep the nutrient in the system, that is, if the fraction of nutrient lost along the herbivore recycling pathway is sufficiently smaller than the fraction of nutrient lost through the plant recycling pathway. This condition is more easily fulfilled if the plant recycling pathway leads to greater losses.

This is illustrated in figure 4: point A1, which corresponds to a pure stand of the plant that is more efficient at recycling, is below point A2, which corresponds to a pure stand of the plant that is less efficient at recycling. Thus, the grazing optimization condition is more stringent and requires a smaller fraction of nutrient lost along the herbivore recycling pathway in the case of A1, when only the plant that is more efficient at recycling is present.

Two Species Present, No Species Replacement: Effect of Community Composition

Only Plant 1 Is Grazed. When only plant 1 is grazed, then

$$\frac{dv_{h1}}{dS_1} = (v_2 - v_1) \frac{R\{l_m + (l_m + k)[v_1 + 2S_2(v_2 - v_1)]\}}{I - l_m R}.$$

For $v_2 > v_1$, the ungrazed plant 2 is less efficient at recycling than the grazed plant type 1. Then dv_{h1}/dS_1 is positive. Thus, the grazing optimization condition is more stringent when the grazed plant is mixed with an ungrazed plant that is less efficient at recycling, as illustrated by curve v_{h1} in figure 4. This is due to the fact that part of the nutrient recycled by herbivores goes to the ungrazed plant, which acts to increase nutrient loss compared with the grazed plant.

For $v_2 < v_1$, the ungrazed plant 2 is more efficient at recycling than the grazed plant 1. Then the derivative dv_{h1}/dS_1 has a sign opposite to that of the previous case for low values of plant 2 frequency. Thus, the grazing optimization condition is less stringent when the grazed plant is mixed with an ungrazed plant whose recycling efficiency is greater. Part of the nutrient recycled by herbivores goes to the ungrazed plant, which acts to decrease nutrient loss compared with the grazed plant. This is again illustrated in figure 4. Curve v_{h2} , showing the condition for grazing optimization when only the plant that is less efficient at recycling is grazed, increases with the frequency of the ungrazed plant, which is more efficient at recycling. But the derivative can change sign for higher values of plant 2 frequency if

$$v_1 > 2v_2 \text{ and } \frac{l_m}{(l_m + k)} < v_1 - 2v_2.$$

Therefore, under certain conditions, the pattern can be inverted at low frequencies of the grazed type.

The Two Plant Types Are Grazed. No general pattern can be found. The threshold fraction of nutrient lost along the herbivore recycling pathway may have a maximum or a minimum when the frequencies of the plant types are changed, depending on herbivore preference, as is shown by curves C1 and C2 in figure 4.

Two Species Present, No Species Replacement: Effect of Herbivore Preference

When two species are present and there is no species replacement, the effect of herbivore preference is

$$\frac{\partial v_{h+}}{\partial \omega_1} = \frac{S_1 S_2 (v_1 - v_2)}{(\omega_1 S_1 + \omega_2 S_2)^2} \left[\frac{I - l_m R + (l_m + k)(v_1 S_1 + v_2 S_2) R}{I - l_m R} \right].$$

The grazing optimization condition becomes more and more stringent as herbivores prefer the plant that is more efficient at recycling. This can be seen in figure 4, since curve C1, which represents the grazing optimization condition when the plant that is more efficient at recycling is preferred, is below curve C2, which represents grazing optimization condition when the plant that is less efficient at recycling is preferred.

Species Replacement

The variation of primary production due to species replacement is

$$\frac{\partial \Phi^*}{\partial S_1} = \frac{I - l_m R}{(v_1 S_1 + v_2 S_2)^2} (v_2 - v_1).$$

If herbivory results in a decreased frequency of the plant that is more efficient at recycling, the condition for grazing optimization becomes even more stringent.

Effect of Plant Depletion Ability

Here we assume that the two plant recycling pathways have the same recycling efficiency:

$$\nu_1 = \nu_2 = \nu_p.$$

Only One Species Present

In a community with only one plant species, the grazing optimization condition is less stringent when the plant is more efficient at depleting the soil mineral nutrient pool. This is illustrated in figure 5A and 5B: point A1, which corresponds to a pure stand of the plant that is more efficient at depleting soil mineral nutrient, is above point A2, which corresponds to a pure stand of the plant that is less efficient at depleting soil mineral nutrient.

Two Species Present, No Species Replacement: Effect of Community Composition

Only One Plant Is Grazed. When only one plant is grazed, then $\partial \nu_{h1} / \partial S_1$ has the sign of $(R_2 - R_1)[l_m - (l_m + k)\nu_p]$.

When the coefficient of migration of mineral nutrient in the soil, k , is small,

$$k < l_m \left(\frac{1 - \nu_p}{\nu_p} \right),$$

the grazing optimization condition, is less stringent when the grazed plant is mixed with a plant that is more efficient at depleting soil mineral nutrient. It is more stringent when the grazed plant is mixed with a plant that is less efficient at depleting soil mineral nutrient. This is illustrated in figure 5A. Curve ν_{h2} , which describes the condition for grazing optimization when only the plant that is less efficient at depleting soil mineral nutrient is grazed, increases with the frequency of the ungrazed plant, which is more efficient at depleting soil mineral nutrient. On the contrary, the grazing optimization condition is more stringent when the grazed plant is mixed with an ungrazed plant that is less efficient at depleting soil mineral nutrient (curve ν_{h1} in fig. 5A).

When the coefficient of migration of mineral nutrient in the soil, k , is large,

$$k > l_m \left(\frac{1 - \nu_p}{\nu_p} \right),$$

the pattern is opposite to the previous one. This is illustrated in figure 5B. Contrary to the previous case, curves ν_{h1} and ν_{h2} decrease with the frequency of the plant that is more efficient at depleting soil mineral nutrient.

The Two Plant Types Are Grazed. The condition for grazing optimization is intermediate between the two conditions when either plant type is grazed. It may become more or less stringent as plant type frequencies change, depending on herbivore preference (curves C1 and C2 in fig. 5A, 5B).

Two Species Present, No Species Replacement: Effect of Herbivore Preference

When two species are present with no species replacement, then $\partial \nu_{h+} / \partial \omega_1$ has the sign of $(R_2 - R_1)$. Grazing optimization becomes easier when the plant that is more efficient at depleting soil mineral nutrient is preferred. This is illustrated in figure 5A and 5B by a comparison of curves C1, showing the grazing optimization condition when the more efficient plant at depleting soil mineral nutrient is preferred, and the lower curves C2, showing the grazing optimization condition when the less efficient plant is preferred.

Species Replacement

For species replacement,

$$\frac{\partial \Phi^*}{\partial S_1} = \frac{l_m(R_2 - R_1)}{\nu_p}.$$

Grazing optimization is facilitated if herbivory results in an increased frequency of the plant that is more efficient at depleting soil mineral nutrient.

APPENDIX C

Correspondence between Our Model and Pastor and Cohen's 1997 Model

This appendix explains the link between our model and Pastor and Cohen's (1997). This comparison enlightens our results and the conditions required for grazing optimization. For every choice of parameters in Pastor and Cohen's (1997) model, corresponding parameters for our model can be computed. If left-hand parameters stand for parameters of our model and right-hand parameters and variables are those of Pastor and Cohen's model: $I = R$, $l_m = e_N$, $a_i = a_p$, $d_i = b_i + e_p$, $d_h = b_c + e_o$

$$\mu_i = \frac{b_i}{b_i + e_i d_D + e_D} \frac{d_D}{d_D},$$

$$\mu_h = \frac{b_c}{b_c + e_c d_D + e_D} \frac{d_D}{d_D},$$

$$\omega_i = \frac{c_i}{c_1 + c_2},$$

$$c = (c_1 + c_2)C^* = (c_1 + c_2) \frac{[(b_2 + e_2)/a_2] - [(b_1 + e_1)/a_1]}{(c_1/a_1) - (c_2/a_2)},$$

$$S_1 = \frac{a_1 x_1^*}{a_1 x_1^* + a_2 x_2^*}.$$

Therefore, our model encompasses all cases explored by Pastor and Cohen, but it can also explore other possibilities due to relaxation of several critical assumptions. Our model differs from Pastor and Cohen's in three respects: local nutrient pools are distinct, plant consumption is donor controlled, and nutrient recycling pathways are distinct for plant and herbivore detritus.

Local Nutrient Pools Are Distinct. In Pastor and Cohen's model, the two plant types share a common homogeneous nutrient pool. Therefore, their coexistence hinges on herbivores (Holt et al. 1994), and the effect of herbivory per se cannot be distinguished from its effect on plant community composition. However, other factors can be responsible for plant coexistence, in particular, the soil is likely to be heterogeneous, and such a heterogeneity allows coexistence of a number of plant species even in the absence of herbivores (Huston and DeAngelis 1994; Loreau 1996, 1998a). This difference in model structure results in different criteria for grazing optimization. In our model, grazing optimization occurs when primary production increases with low rates of herbivory. The structure of Pastor and Cohen's model does not allow varying grazing intensity because grazing intensity is the result of the dynamic equilibrium between the two plant species and the herbivore; that is, it is constrained by plant species coexistence. Therefore, grazing optimization in their model requires that primary production at a given consumption rate be higher than that without herbivores, a condition that is more stringent than ours. However, in a model identical to theirs in this respect, but with uncoupled detritus pathways, grazing optimization can be obtained with the following parameters: $d_h = 1.8$ kg N ha⁻¹ yr⁻¹ and $\mu_h = 0.9$.

Plant Consumption Is Donor Controlled. We use donor-controlled herbivory for the sake of simplicity. Appendix A

shows that identical results are obtained with a Lotka–Volterra interaction, in spite of the fact that the equations are far more complicated in the latter case.

Nutrient Recycling Pathways Are Distinct for Plant and Herbivore Detritus. Plant palatability has been shown to affect plant detritus decomposition (Grime et al. 1996). Therefore, detritus of the different plant types should follow different dynamics, and hence should also be subject to different fractions of nutrient loss during recycling. Herbivore detritus is even more likely to be different from plant detritus; for example, urine is already mineralized and is subject to volatilization (Schimel et al. 1986). In our model, all these different detritus follow different pathways, whereas in Pastor and Cohen, they all went to a common detritus pool, and their decomposition followed the same dynamics.

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