

Plant–herbivore interactions and ecological stoichiometry: when do herbivores determine plant nutrient limitation?

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Abstract

Recent studies on plant–herbivore indirect interactions via nutrient recycling have led to the hypothesis that herbivores with a low nitrogen: phosphorus ratio, feeding on plants with a higher nitrogen: phosphorus ratio, recycle relatively more nitrogen, driving plants into phosphorus limitation. We demonstrate in this paper that such a hypothesis is valid only under restricted conditions, i.e. the nitrogen: phosphorus ratio of inorganic nutrients supplied to the system must be neither too high nor too low compared with the nitrogen: phosphorus ratio of the whole plant + herbivore biomass. If plants have a greater affinity for phosphorus than for nitrogen, low herbivore nitrogen: phosphorus ratio can even promote nitrogen limitation. These results are qualitatively robust, whether grazing functions are donor-controlled or recipient-controlled. We present a graphical analysis of these conditions based on the Zero Net Growth Isocline method.

Keywords

Herbivory, stoichiometry, nutrient cycling, nutrient limitation.

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INTRODUCTION

Stoichiometric considerations of chemical elements in stocks and fluxes of biomass have long been addressed in ecosystem ecology (Lotka 1925; Redfield 1958; Reiners 1986; Elser *et al.* 1996; Hessen 1997), but recent advances have raised new questions on the implications of ecological stoichiometry for the functioning of both aquatic and terrestrial ecosystems (Sternner *et al.* 1992; Elser *et al.* 1996; Elser & Urabe 1999; Daufresne & Loreau in press). Ecological stoichiometry states that mass-balance constraints for chemical elements must be met at the scale of ecological interactions such as competition, predation and herbivory (Elser *et al.* 1996). Nitrogen (N) and phosphorus (P) have been mostly considered, because these elements are known to limit primary production in most terrestrial and aquatic ecosystems (Rosswall 1976; Hecky & Kilham 1988; Downing & McCauley 1992). Our knowledge about herbivory suggests that direct and indirect interactions between plants and herbivores are strongly affected by mass-balance constraints of chemical elements such as carbon (C), N and P (Hessen & Andersen 1992; Urabe 1995). Recent studies have shown that herbivore growth can be limited by food mineral content rather than by food energy content, highlighting the importance of food

quality vs. food quantity for consumer reproductive success and dynamics (Hessen 1992; Sternner 1993; Sternner *et al.* 1993; Huxel 1999). As an example, several studies indicate that P limitation of freshwater zooplankton may be common in limnetic ecosystems. Urabe (Urabe *et al.* 1997) quantified this limitation and provided experimental evidence that for a food with an atomic C : P ratio higher than 300, *Daphnia* growth is P limited rather than energy limited.

Empirical and experimental data support homeostatic regulation of N and P in planktonic herbivores entailing strict N:P ratios in biomass (Hessen 1990; Andersen & Hessen 1991; Hessen & Lyche 1991). These ratios show little intraspecific, but strong interspecific variations (Burns 1975; Andersen & Hessen 1991; Hessen & Lyche 1991). Since nutrient limitation of zooplanktonic taxa should be affected by their N:P ratio compared with their food's N:P ratio, Koski (1999) hypothesized that cladocerans with a high P content should be commonly P limited, while copepods which contain more N should be N limited.

During the last decade, the stoichiometric approach has also focused on indirect interactions between plants and herbivores via nutrient cycling (Elser & Urabe 1999). Experimental data and mass-balance models suggest that zooplanktonic herbivores mainly maintain N and P

homeostasis by differential excretion of N and P, even though other mechanisms such as ingestion of inorganic phosphorus cannot be excluded (Urabe *et al.* 1997). Differential excretion of N and P is determined by the difference between the N:P ratio of herbivores and the N:P ratio of the food they ingest (Olsen *et al.* 1986; Sterner 1990; Urabe 1993). Consequently, Sterner (1990) hypothesized that N and P recycling by herbivores may play a key role in nutrient availability for plants: a zooplankton that is richer in P than the algae it ingests should retain relatively more P than N, and thus recycle relatively more N, driving the algae into P limitation. Such a control of plant nutrient limitation by herbivores may have potentially strong consequences for resource competition for both plants and herbivores, and may be key for our understanding of aquatic as well as terrestrial plant–herbivore interactions and successional processes. Rothhaupt (1997), however, argued that homeostasis in herbivores was not sufficient to grant the control of plant limitation. He added the prerequisite that nutrients recycled by zooplankton form a significant share of the growth demands of algae. He stated that this requirement should often be met in the euphotic zone of lake ecosystems, because nutrient concentration is often low and the supply from deeper strata and external sources is minimal (Wetzel 1983). On the other hand, according to Andersen (1997), the main condition required for Sterner’s hypothesis is that the N:P ratio in nutrient supply must be contained within a restricted range. Using a stoichiometrically explicit algae–*Daphnia* model parameterized with empirical data, he showed that only few temperate lakes may respect this condition. Thus, at least for natural limnetic ecosystems, Sterner’s hypothesis would hold only in restrictive cases. Except Andersen’s (1997) work, which concerns a very specific algae–*Daphnia* model, no theoretical approach has assessed the general conditions under which Sterner’s hypothesis holds. Yet, the determinism of plant limitation by two potential limiting nutrients, in the absence of grazers, has long been addressed in theoretical and experimental studies (Tilman 1982). This has led to emphasize the role of the ratio of nutrients supplied to the system, i.e. the ratio of the so-called “supply point”, highlighted by a graphical method using the plant Zero Net Growth Isocline (Tilman 1982). Hence, when the plant is grazed, we argue that the role of the herbivore should be reconsidered, taking into account the system-level requirements. We address in this paper the conditions under which Sterner’s hypothesis holds, i.e. a herbivore controls plant nutrient limitation, when two nutrients are potential limiting factors for the plant growth. We examine the classic example of a herbivore with a low N:P feeding on a plant with a higher N:P, in a chemostat system. For this

purpose, we first present a plant–herbivore model that is stoichiometrically explicit in terms of N and P. The model includes direct (predation) as well as indirect (nutrient recycling) interactions between the plant and the herbivore. Second, we compare the conditions for P limitation when the plant is alone and when it is grazed by the herbivore, to determine when Sterner’s hypothesis is expected to be met. Finally, we propose a graphical analysis of these conditions, based on the Zero Net Growth Isocline method (Tilman 1982).

THE MODEL

We present here a general compartment model for a plant–herbivore chemostat-like system that couples the cycles of two nutrients, N (nitrogen) and P (phosphorus) (Fig. 1). The model is made up of 6 dynamic variables:

- 3 compartments of N: N_i , the inorganic stock of N available to the plant, N_p , the quantity of N contained in plant biomass and N_h , the quantity of N contained in herbivore biomass.
- 3 compartments of P: P_i , the inorganic stock of P available to the plant, P_p , the quantity of P contained in plant biomass and P_h , the quantity of P contained in herbivore biomass.

N and P are coupled into the biomass by constant N : P ratios, α for the plant and β for the herbivore. The N : P ratio is lower in the herbivore than in the plant, so that $\alpha > \beta$.

The dynamic equations for the 6 variables are:

$$\frac{dN_i}{dt} = a(S_N - N_i) - (F_N(N_p, N_i, P_i) - r_p N_p - \eta_h N_h - W_N(N_p, N_h)) \quad (1a)$$

$$\frac{dP_i}{dt} = a(S_P - P_i) - \left(\frac{F_N(N_p, N_i, P_i)}{\alpha} - \frac{r_p N_p}{\alpha} - \frac{\eta_h N_h}{\beta} \right) \quad (1b)$$

$$\frac{dN_p}{dt} = (F_N(N_p, N_i, P_i) - r_p N_p) - (H_N(N_p, N_h) + aN_p) \quad (1c)$$

$$\frac{dP_p}{dt} = \frac{1}{\alpha} \left((F_N(N_p, N_i, P_i) - r_p N_p) - (H_N(N_p, N_h) + aN_p) \right) \quad (1d)$$

$$\frac{dN_h}{dt} = H_N(N_p, N_h) - \eta_h N_h - W_N(N_p, N_h) - aN_h \quad (1e)$$

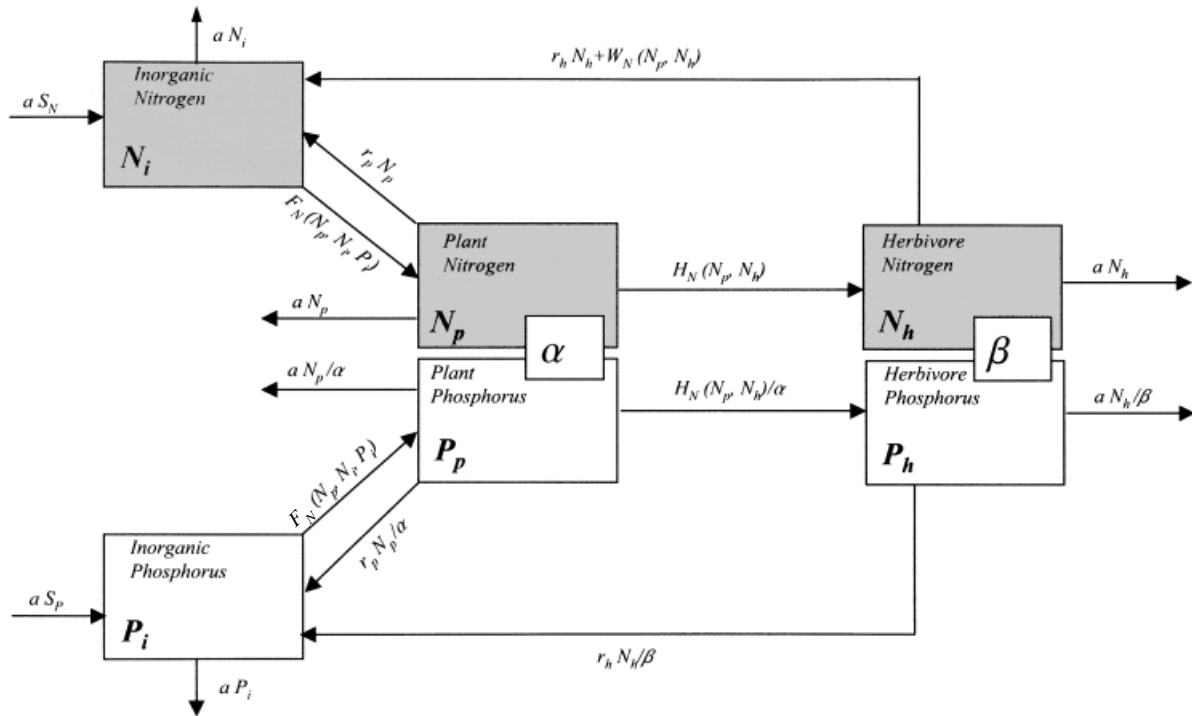


Figure 1 Flow diagram of the plant–herbivore model. The model couples the cycles of nitrogen (in grey) and phosphorus (in white). It is made up of 3 compartments of nitrogen: N_i , the inorganic stock of nitrogen available to plants, N_p , the quantity of nitrogen contained in the plant biomass, and N_h , the quantity of nitrogen contained in the herbivore biomass, and three compartments of phosphorus: P_i , the inorganic stock of phosphorus available to plants, P_p , the phosphorus contained in plant biomass, and P_h , the phosphorus contained in herbivore biomass. Nitrogen and phosphorus are coupled in the biomass of the plant and the herbivore by the constant ratio α and β , respectively. The ratio is different for the plant and the herbivore; here $\alpha > \beta$. The system models a chemostat, with a constant dilution rate a . $a S_N$ and $a S_P$ are the inflows of nutrients (nitrogen and phosphorus, respectively) to the system. $a N_i$, $a N_p$ and $a N_h$ are the outflows of nitrogen, from the inorganic pool, plant biomass, and herbivore biomass, respectively. $a P_i$, $a N_p/\alpha$ and $a N_h/\beta$ are the outflows of phosphorus, from the inorganic pool, plant biomass, and herbivore biomass, respectively. $F_N(N_p, N_i, P_i)$ and $F_N(N_p, N_i, P_i)/\alpha$ are the plant nutrient flows for nitrogen and phosphorus, respectively. $H_N(N_p, N_h)$ and $H_N(N_p, N_h)/\alpha$ are the flows of nitrogen and phosphorus, respectively, associated with herbivore grazing. $r_p N_p$ and $r_p N_p/\alpha$ are the nitrogen and phosphorus flows, respectively, recycled by the plant. $r_h N_h + W_N(N_p, N_h)$ and $r_h N_h/\beta$ are the nitrogen and phosphorus flows, respectively, recycled by the herbivore.

$$\frac{dP_h}{dt} = \frac{H_N(N_p, N_h)}{\alpha} - \frac{r_h N_h}{\beta} - \frac{a N_h}{\beta} \tag{1f}$$

where a is the chemostat dilution rate, r_p and r_h are the nutrient recycling rates (by excretion and natural mortality) of the plant and the herbivore, respectively, and S_N and S_P are the concentrations of inorganic N and P, respectively, supplied to the system. $F_N(N_p, N_i, P_i)$ is the flux of N associated with plant nutrition, $H_N(N_p, N_h)$ is the flux of N associated with plant consumption by the herbivore, and $W_N(N_p, N_h)$ is the flux of nitrogen excreted by the herbivore to maintain its homeostasis.

At equilibrium, the constant dilution rate a implies that the total nutrient content of the system equals the quantity supplied to the system:

$$S_N = N_i^* + N_p^* + N_h^* \tag{2a}$$

and

$$S_P = P_i^* + P_p^* + P_h^* \tag{2b}$$

where the star denotes equilibrium values.

Plant N : P regulation

Plant homeostasis implies that the $N_p:P_p$ ratio stays constant (equal to α). This condition is:

$$\frac{dN_p}{dt} = \alpha \frac{dP_p}{dt} \tag{3}$$

According to Tilman (1982), plant homeostasis is ensured by the control of nutrient uptake. This is the assumption we made in equation (1), where the inflow of

P to the plant equals the inflow of N divided by the plant ratio α .

Herbivore N : P regulation

Herbivore homeostasis implies that:

$$\frac{dN_h}{dt} = \beta \frac{dP_h}{dt} \quad (4)$$

Herbivores usually maintain homeostasis by differential assimilation, so that they excrete the surplus of nutrient contained in the food they ingest (Sternner 1990). The herbivore ingests N and P coupled into the plant ratio α . Substitution of equations (1e) and (1f) into (4) provides the flux of N excreted by the herbivore to maintain its ratio β :

$$W_N(N_p, N_h) = \frac{\alpha - \beta}{\alpha} H_N(N_p, N_h) \quad (5)$$

Condition for plant P limitation

We express N and P plant nutrition fluxes as minimum functions following Liebig's law (Grover 1997):

$$F_N(N_p, N_i, P_i) = \min [f_N(N_i, N_p), \alpha f_P(P_i, N_p)] \quad (6)$$

where f_N is the nutrition flux of N when the plant is N limited, and f_P is the nutrition flux of P when the plant is P limited.

We define f_N and f_P in a simple Lotka–Volterra fashion:

$$f_N(N_i, N_p) = n_N N_i N_p \quad (7)$$

$$f_P(P_i, N_p) = n_P P_i N_p \quad (8)$$

where parameters n_N and n_P are the specific plant nutrition rates for N and P, respectively. Such expressions for f_N and f_P have the same properties with regard to the nutrient limitation conditions than do more complex Monod equations, and they keep the model more tractable. At equilibrium, the ratio between $f_N(N_i^*, N_p^*)$ and $\alpha f_P(P_i^*, N_p^*)$ determines the switching from N to P limitation. Thus, the condition for P limitation at equilibrium is:

$$\frac{f_N(N_i^*, N_p^*)}{f_P(P_i^*, N_p^*)} > \alpha \quad (9)$$

RESULTS

To address the issue of the herbivore contribution to plant P limitation, we first assess the condition for P limitation when the plant is alone. We then compare it with the condition when the herbivore is present.

Plant alone

Equation (1) without the herbivore [by setting $N_h, P_h, H_N(N_p, N_h)$ and $W_N(N_p, N_h)$ to zero] represent the situation where the plant is free from grazing. As shown in the Appendix, the system is able to reach two stable nontrivial equilibria: one for which the plant is P limited and the other for which it is N limited.

Substituting equation (2) into condition (9) with N_h and P_h set to 0 leads to the following condition for P limitation at equilibrium:

$$S_N > \alpha S_P + (j - 1) \alpha P_{i1}^* \quad (10)$$

where P_{i1}^* is the equilibrium value of P_i when P limits plant growth, equivalent to the R^* defined by Tilman (1982), and j is the ratio between the plant affinities for P and N:

$$j = n_P/n_N \quad (11)$$

As shown in the Appendix, the equilibrium value for the inorganic N pool when N is the limiting resource for plant growth is:

$$N_{i1}^* = (a + r_p)/n_N \quad (12)$$

When P is limiting, the equilibrium value for the inorganic P pool is:

$$P_{i1}^* = \frac{(a + r_p)}{\alpha n_P} \quad (13)$$

Thus, the ratio $N_{i1}^*/P_{i1}^* = \alpha j$.

Condition (10) for P limitation can be analysed graphically following Tilman's (1982) method. Equation (1a) and (1b) can be translated into the following vector equation:

$$\begin{bmatrix} \frac{dN_i}{dt} \\ \frac{dP_i}{dt} \end{bmatrix} = a \underbrace{\begin{bmatrix} S_N - N_i \\ S_P - P_i \end{bmatrix}}_{\vec{u}} + \underbrace{\begin{bmatrix} r_p N_p - F_N(N_p, N_i, P_i) \\ \frac{r_p N_p}{\alpha} - \frac{F_N(N_p, N_i, P_i)}{\alpha} \end{bmatrix}}_{\vec{c}} \quad (14)$$

The first vector of the right side of this equation, noted \vec{u} , is the supply vector as defined by Tilman (1982). The second vector, noted \vec{c} , includes plant uptake ($F_N(N_p, N_i, P_i)$) and plant recycling ($r_p N_p$) components. In Tilman (1982) this second vector was called the "consumption vector" but recycling was not considered. Here we include a recycling component, so that \vec{c} represents the net consumption of nutrients by the plant (consumption minus recycling). By reference to Leibold (1996), we call it the "impact vector" of the plant on nutrients.

Examples of vectors \vec{c} and \vec{u} in the (P_i, N_i) plane are represented in Fig. 2. The growth isocline along which nutrient inflow equals nutrient outflow in the plant population is the one for which $dN_p/dt = 0$ and $dP_p/dt = 0$.

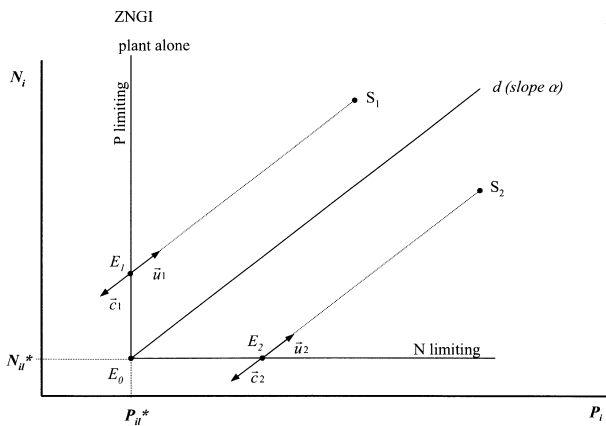


Figure 2 Graphical analysis of the model for a plant without grazing growing with two essential nutrients N_i and P_i . The coordinates represent the quantities of inorganic N and P in the system. The ZNGI is made up of the “N limiting” (vertical) and “P limiting” (horizontal) solid lines. These two lines cross at the point $E_0 = (P_{ih}^*, N_{ih}^*)$, where plant growth is exactly colimited by N and P, with $N_{ih}^* = \alpha j P_{ih}^*$. Any equilibrium point in the (N_i, P_i) plane must lie on the ZNGI. At this point, the impact vector \vec{c} exactly balances the supply vector \vec{u} . Supply points that lie between the axes and the ZNGI are unable to support the plant at equilibrium. Supply points that lie above the ZNGI allow plant persistence with either P or N limitation at equilibrium. Since the slope of the impact vector \vec{c} at equilibrium is α , any supply point lying above the line d with slope α , such as supply point S_1 , leads to P limitation (equilibrium point E_1), whereas it leads to N limitation (equilibrium point E_2) if it lies below d , such as supply point S_2 .

$dt = 0$. It is called the Zero Net Growth Isocline (ZNGI), and is defined by N_{ih}^* and P_{ih}^* . Any equilibrium point of the plant–nutrient system lies on the ZNGI. For such an equilibrium point, net resource consumption balances resource supply, so that \vec{u} and \vec{c} have the same slope and length, but opposite directions. The supply vector \vec{u} points towards the supply point (S_p, S_N) , while the impact vector \vec{c} points towards the P_i and N_i axes. Owing to plant homeostasis, the slope of \vec{c} is α . Thus, for any supply point (S_p, S_N) , the equilibrium point lies at the intersection between the ZNGI and the straight line with slope α that passes through the supply point. Whether the plant is N or P limited at equilibrium depends on the location of the equilibrium point on the ZNGI. If the equilibrium lies at the corner of the ZNGI [point $E_0 = (P_{ih}^*, N_{ih}^*)$], the plant is exactly colimited by N and P. Thus, condition (10) for P limitation can be interpreted graphically as the area of supply points that lie above the line d whose slope is α and which crosses the ZNGI at its corner E_0 :

$$d: S_N = \alpha S_p + (j - 1) \alpha P_{ih}^* \quad (15)$$

Thus, any supply point that lies above line d (point S_1 on Fig. 2) leads to P limitation (equilibrium point E_1).

Plant grazed by a herbivore with a low N:P ratio

Consider now the whole model, including the herbivore. For simplicity, assume that grazing $H_N(N_p, N_h)$ is donor-controlled:

$$H_N(N_p, N_h) = b N_p \quad (16)$$

With such a donor-controlled function, herbivore biomass is simply proportional to plant biomass at equilibrium. The equilibrium values and the stability analysis are presented in the Appendix. When N is limiting, the equilibrium value for the inorganic N stock is:

$$N_{ih}^* = \frac{a + \eta_h + b}{\eta_N} \quad (17)$$

Similarly, when P is limiting, the equilibrium value for the inorganic P stock is:

$$P_{ih}^* = \frac{a + \eta_h + b}{\alpha \eta_P} \quad (18)$$

Thus, the ratio $N_{ih}^*/P_{ih}^* = \alpha j$. The herbivore does not change this ratio because N and P are coupled into the ratio α in the herbivore consumption flow.

Substituting equation (2) into condition (9) leads to the following condition for P limitation at equilibrium:

$$S_N > \delta^* S_p + (\alpha j - \delta^*) P_{ih}^* \quad (19)$$

where δ^* is the N:P ratio of the whole living system (plant + herbivore) at equilibrium:

$$\delta^* = \frac{N_p^* + N_h^*}{P_p^* + P_h^*} \quad (20)$$

Comparing conditions (19) and (10) graphically highlights the role of the herbivore in the plant limitation status (Fig. 3). The herbivore induces two main changes:

- 1 A translation of the ZNGI. This is a classical result of grazing. The herbivore increases plant mortality, and thus the plant must compensate this additional loss by increasing its nutrition flow, leading to higher nutrient stocks at equilibrium. As shown above, however, this increase does not change the N:P ratio of inorganic nutrients at equilibrium when the plant is colimited, which stays equals to αj .

2 A change in the slope of the impact vector \vec{c} :

$$\vec{c} = \left[\begin{array}{c} r_p N_p + \eta_h N_h + W_N(N_p, N_h) - F_N(N_p, N_i, P_i) \\ \frac{r_p N_p}{\alpha} + \frac{\eta_h N_h}{\beta} - \frac{F_N(N_p, N_i, P_i)}{\alpha} \end{array} \right] \quad (21)$$

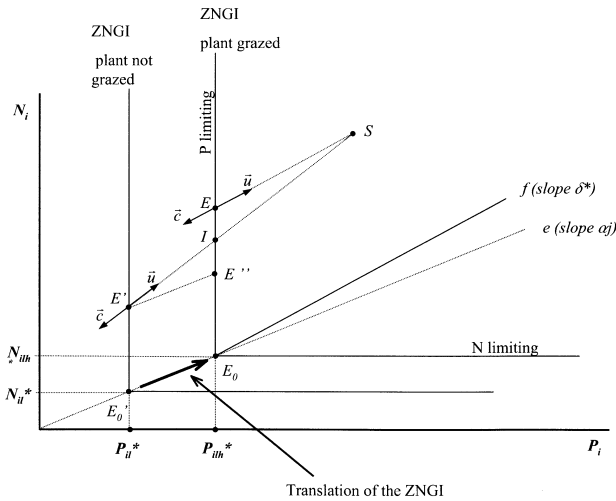


Figure 3 Graphical analysis of the model for a plant growing with two essential nutrients N_i and P_i and grazed by a herbivore. By comparison with the previous case (Fig. 2), herbivore grazing results in a translation of the ZNGI along the line e with slope αj , defining a new ZNGI (plant grazed ZNGI). Supply points situated below the new ZNGI are unable to support the plant–herbivore system. Supply points situated above the ZNGI lead either to P or N limitation of plant growth at equilibrium. The slope of the new impact vector \vec{c} at equilibrium is δ^* , the N : P ratio of the whole plant + herbivore biomass, with δ^* taking any value between α and β . Hence supply points lying above the line f with slope δ^* lead to P limitation, whereas those lying below f lead to N limitation. The supply point S represented on the figure leads to the equilibrium point E' for the plant in the absence of the herbivore. When the plant is grazed, it moves to the new equilibrium point E situated at the intersection between the plant grazed ZNGI and the new impact vector \vec{c} . The point I represents the virtual equilibrium in the case of $\delta^* = \alpha$ (i.e. the herbivore has the same ratio as the plant). The point E'' is the projection of E' on the new ZNGI with slope αj . Thus, the distance from E'' to I represents the contribution of ZNGI translation in promoting P limitation, whereas the distance from I to E represents the contribution due to the change in the impact vector slope.

Note that \vec{c} now describes the plant + herbivore net consumption of N_i and P_i , so that it can be regarded as the impact vector of the plant–herbivore community on the resources N_i and P_i . Substituting equations (1c), (1d), (1e) and (1f) into (21), one can easily demonstrate that at equilibrium the slope of \vec{c} is δ^* , the N:P ratio of the whole living system.

The more herbivore biomass dominates at equilibrium, the closer δ^* is to β , whereas the more plant biomass dominates, the closer δ^* to α . Also, if β tends to α , δ^* eventually tends to α . As a consequence, the value of δ^* is bounded by α and β . Graphically, the area of supply points leading to P limitation lies above the line f with slope δ^* which crosses the ZNGI at its corner:

$$f: S_N = \delta^* S_P + (\alpha j - \delta^*) P_{\text{ilh}}^* \quad (22)$$

The ZNGI translation or the change in the slope of \vec{c} promote P limitation if either they make the equilibrium point tend to the ZNGI corner (i.e. to colimitation by N and P) when the plant is N limited, or they increase the distance to the ZNGI corner when the plant is P limited. For equilibrium points close enough to colimitation, they can promote a qualitative shift from N to P limitation. Note that the change in the slope of \vec{c} always promotes P limitation because, by definition, $\beta < \alpha$ (Figs 4 and 5). On the other hand, the ZNGI translation does not depend on β , and thus can promote either N or P limitation, depending on the plant affinity (ratio j).

1 When the plant has a greater affinity for N ($j < 1$), the ZNGI translation and the change in the slope of the impact vector \vec{c} are synergistic in promoting P limitation (Fig. 4). The larger the grazing rate h , the closer δ^* is to β , the stronger the ZNGI translation, and thus the stronger the promotion of P limitation (see equilibrium values in the Appendix). The indirect effect of the herbivore through nutrient recycling is then convergent with its direct effect through grazing which determines δ^* . A nutrient limitation shift is possible only from N to P and in a restricted range of N : P supply ratios, determined by lines d and f (Fig. 4).

2 When the plant has a greater affinity for P ($j > 1$), the ZNGI translation promotes N limitation, whereas the change in the slope of the impact vector \vec{c} promotes P limitation. The two effects balance each other at the intersection point of lines d and f with abscissa S_{Pcross} :

$$S_{\text{Pcross}} = \frac{(\alpha j - \delta^*) P_{\text{ilh}}^* - (\alpha j - \alpha) P_{\text{il}}^*}{\alpha - \delta^*} \quad (23)$$

Thus, the herbivore promotes either N or P limitation (Fig. 5): for a phosphorus supply lower than S_{Pcross} , the ZNGI effect outweighs the impact vector effect and the herbivore promotes N limitation. For a higher phosphorus supply, on the contrary, the herbivore promotes P limitation.

For a restricted range of N:P ratios determined by lines d and f , the herbivore induces a limitation shift: a shift from N to P limitation if P supply is higher than S_{Pcross} and from P to N if it is lower.

For more complex grazing functions than the simple donor-controlled function used above, equations (19)–(23) stay unchanged because they do not depend on the grazing function. However, since the latter determines the equilibrium values P_{ilh}^* and δ^* , it plays a quantitative role in plant nutrient limitation. For example, with recipient-controlled functions, such as a Lotka–Volterra function, the equilibrium values for inorganic nutrient (N_{ilh}^* and P_{ilh}^*) and herbivore (N_{h}^* and P_{h}^*) stocks change with the

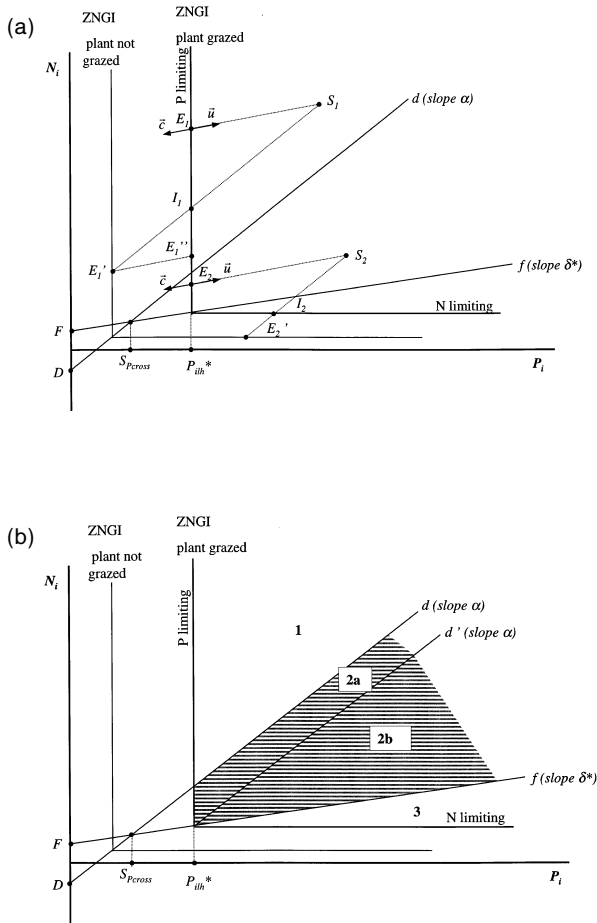


Figure 4 Graphical analysis of the model for a plant growing with two essential nutrients N_i and P_i , and grazed by a herbivore. Grazing is donor-controlled. The plant has a greater affinity for N than for P ($j < 1$). (a) Since $j < 1$, the threshold P supply S_{Pcross} is lower than P_{ill}^* . Thus, the ZNGI translation always promote P limitation. This is illustrated in the figure by the fact that I_1 lies above E_1'' . In addition the change in the slope of \vec{c} also promotes P limitation so that the two effects are synergistic. Note that for supply points that lie between lines d and f , such as point S_2 , the induction of P limitation leads to a shift from N to P limitation (E_2' is N limited but E_2 is P limited). (b) As a result, the area of supply points above the ZNGI can be divided into zones defined by the lines d , d' and f :

1 Two “no shift” zones (white zones 1 and 3) in which the herbivore does not promote shift from limitation by one nutrient to limitation by another at equilibrium. A plant, that is either P (zone 1) or N (zone 3) limited in the absence of herbivory remains limited by the same nutrient when grazed by the herbivore, because the supply ratio $S_N : S_P$ is too high or too low to allow the herbivore to induce a shift. Note that if the plant is P limited, the herbivore increases P limitation, and when it is N limited, it decreases N limitation.

2 “Shift” zones (grey zones horizontally hashed 2a and 2b) in which the supply ratio $S_N : S_P$ is contained into a range that allows the herbivore to promote a shift from N to P limitation. These zones are delimited by line d with slope α that crosses the N_i -axes at point $D [0, (j - 1) \alpha P_{ill}^*]$, and line f with slope δ^* that crosses the N_i -axes at point $F [0, (\alpha j - \delta) P_{ill}^*]$. For zone 2a, the ZNGI translation alone is sufficient to promote the shift to P limitation. For zone 2b, the ZNGI translation itself is not sufficient and requires the addition of the impact vector effect to enhance the shift to P limitation.

nutrient supply concentrations (see Appendix). In this case, the ZNGI translation and the slope of the impact vector \vec{c} both change with supply concentrations, but the pattern of limitation described above remains valid.

DISCUSSION

The analysis of the stoichiometrically explicit model of plant–herbivore interactions presented in this paper clearly demonstrates the conditions under which a herbivore with a low N:P ratio induces a qualitative limitation shift (i.e. the plant is N limited when alone, but P limited when grazed by the herbivore). These conditions depend on whether the plant has a greater affinity for N or for P: (1) when the plant has a greater affinity for N ($j < 1$), the herbivore always promotes P limitation, and the conditions for a qualitative limitation shift are as follows: the N:P ratio in the nutrient supply to the system must be neither too high nor too low compared with the N:P ratio of the whole plant + herbivore biomass. On the other hand (2) when the plant has a

greater affinity for P ($j > 1$), the herbivore can either promote N or P limitation, depending on P supply. If the P load is higher than a threshold value, the herbivore promotes P limitation. The conditions required for shifting from N to P or P to N limitation are the same as in (1).

These results show that the conditions for herbivore-mediated nutrient limitation depend on the whole living system as a global stock of nutrient unavailable for plant nutrition, and not only on the N : P ratio recycled by the herbivore. The lower the herbivore N : P ratio, however, the easier the conditions are met. Thus, the conditions are not purely stoichiometric, because they involve the biological interaction between the plant and the herbivore. As mentioned in the introduction, Rothhaupt (1997) argued that an essential prerequisite to Sterner’s hypothesis was that nutrients recycled by zooplankton form a significant share of the growth demands of algae. For Andersen (1997), the main condition required was that the loading N : P ratio must be contained in a restricted range. The conditions resulting from our model integrate those

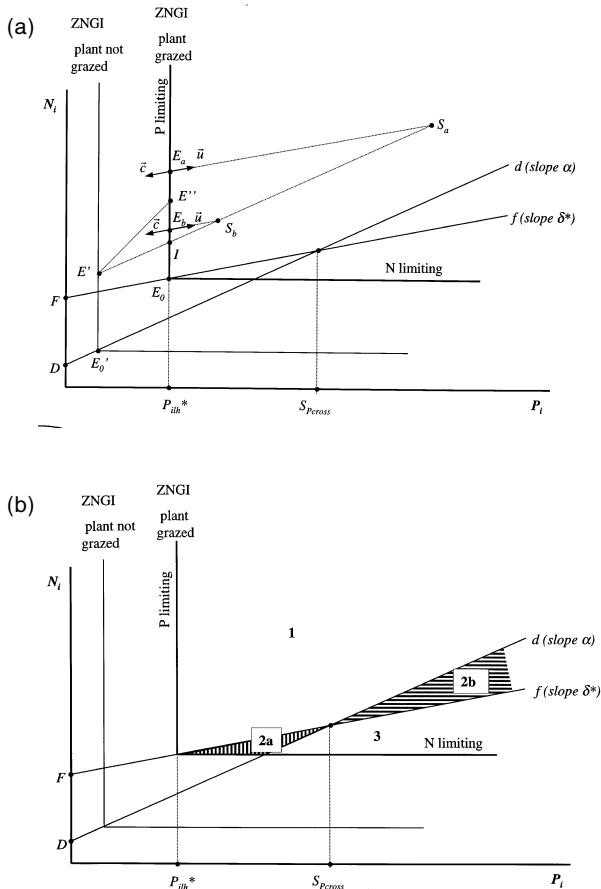


Figure 5 Graphical analysis of the model for a plant growing with two essential nutrients N_i and P_i , and grazed by a herbivore. Grazing is donor-controlled, and the plant has a greater affinity for P than for N ($j > 1$). (a) Since $j > 1$, the threshold P supply $S_{P_{cross}}$ is higher than P_{ih}^* . This implies that the ZNGI translation promotes N limitation, whereas the change in the slope of \vec{c} from α to δ^* promotes P limitation. Thus, the two effects are antagonistic and the net effect of the herbivore will depend on which effect is dominant. For supply points with $S_p > S_{P_{cross}}$, such as point S_a , the net effect is to promote P limitation, because the effect of the impact vector is strong enough to outweigh the effect of the ZNGI. This is illustrated in the figure by the fact that the equilibrium point E_a lies above point E'' . On the other hand, for supply points with $S_p < S_{P_{cross}}$, such as S_b , the effect of the impact vector is not strong enough so that the net effect of the herbivore is to promote N limitation. This is illustrated by the fact that E_b lies below E'' . (b) As for Fig. 4(b), the area of supply points above the ZNGI can be divided into 4 zones:

- 1 Two “no shift” zones (white zones 1 and 3) in which the herbivore does not promote limitation shift at equilibrium. A plant that is either P (zone 1) or N (zone 3) limited in the absence of herbivory remains P or N limited when grazed by the herbivore. Herbivory promotes either an increase or a decrease of the nutrient limitation depending on whether the P supply is above or below the threshold $S_{P_{cross}}$.
- 2 One “N shift” zone (vertically hatched zone 2a) in which the plant is P limited in the absence of herbivory and N limited when grazed.
- 3 One “P shift” zone (horizontally hatched zone 2b) in which the plant is N limited when alone and P limited when grazed.

of Andersen (1997) and Rothhaupt (1997), in that they require that (1) the N:P ratio of inorganic nutrients supplied to the system be constrained within a certain range, and (2) herbivore biomass be large enough compared with plant biomass, which implies at equilibrium that the herbivore’s contribution to nutrient recycling be sufficient to determine the plant nutrient limitation status. Our results also show that a herbivore with a low N:P can either enhance P or N limitation. The second possibility contradicts Sterner’s (1990) hypothesis. It seems counterintuitive that a herbivore with a low N : P ratio can enhance N limitation, but the graphical representation proposed in this paper clearly shows the two mechanisms by which the herbivore influences plant nutrient limitation: isocline translation and change in the slope of the impact vector. Those two mechanisms can play either synergistic or antagonistic roles, depending on plant affinities for P and N. Thus, a herbivore with a low N : P ratio should promote P limitation if the plant has a greater affinity for N, but promote either P or N limitation if the plant has a greater affinity for P.

These results are qualitatively robust to a change in the grazing function, because they only depend on N and P mass-balance constraints at equilibrium. However, the direct and indirect plant–herbivore interactions are closely linked, in that the direct interaction determines both the plant and herbivore biomass at equilibrium, which in turn determine the role of the herbivore for plant nutrient limitation. Thus, the grazing function plays a quantitative role by determining the plant:herbivore biomass ratio at equilibrium.

The Lotka–Volterra functions used in our model lead to stable equilibria. One could argue that this is an oversimplification of resource–consumer dynamics, since other nonlinear functions such as Monod’s are able to lead to more complex dynamics such as stable limit cycles. It is easy to demonstrate that using Monod functions for nutrient consumption by the plant leads to similar results as do Lotka–Volterra functions with regard to equilibrium values and limitation status. The only difference is that with Monod functions the system is able to oscillate around the equilibrium values, but both the ZNGI

translation and the change in the impact vector occur. Thus, if the amplitude of these oscillations are small enough so that they do not interfere with the limitation shift, the results should be qualitatively similar. Further work, however, would be necessary on this issue.

Another criticism that could be addressed to our model is that we assume strict homeostasis in the plant. This is a strong assumption because (1) the C : N : P ratio in plants is known to fluctuate in a specific range depending on inorganic nutrient availability, and (2) the herbivore growth rate is known to fluctuate with this ratio which represents the food quality. The impact of these fluctuations in plant–herbivore dynamics was addressed by Andersen with his algae–*Daphnia* model coupling C and P (Andersen 1997). For a range of nutrient supply and dilution rates, the flexibility of the food quality and the response of the *Daphnia* entails oscillations of alga and *Daphnia* biomasses. Again, we can only speculate that the smaller the amplitude of the fluctuations, the more likely our results will hold. This is another issue on which more research would be needed.

A last criticism concerning the assumptions underlying our model is that this does not take into account the decomposer community. The model follows the aquatic plant–herbivore models developed by Sterner and Andersen, which postulate that the recycling role of the decomposer community is low in pelagic systems (Andersen 1997). However, studies concerning the microbial loop suggest that bacteria and protists can represent a substantial stock of organic matter in aquatic ecosystems (Azam *et al.* 1983; Amblard *et al.* 1998). If this is the case, decomposers may also play a role in determining the plant nutrient limitation status by their ability to stock N and P. They should be considered in future models. Despite these limitations, our model makes useful hypotheses on the circumstances under which herbivores with a low N : P ratio are expected to control the plant nutrient limitation status in nature. For example, the control of algal biomass by herbivorous cladocerans is common in freshwater systems, at least during transient periods called “clear-water phases” by limnologists. In a moderately eutrophic lake, Lampert (1986) showed that during such phases when *Daphnia* dominates the zooplanktonic herbivore community, total zooplankton biomass can reach 0.7 mg dry weight L⁻¹, which corresponds (Rothhaupt 1997) to more than 60% of the total P of the system. Thus clear-water phases in a lake with N and P natural loads close to the algal optimum N : P ratio should be suitable environments for herbivore control on plant nutrient limitation. On the contrary, such a control is unlikely in algal bloom phases with a low density of zooplankton in lakes with N and P loads far from the algal optimum N : P ratio.

We arbitrarily chose herbivores with a low N : P ratio in this paper in order to simplify and clarify the demonstration. Obviously, we could as well apply our method to a symmetrical situation where herbivores have a high N:P ratio.

Our results suggest that the determinism of nutrient limitation involves complex processes: external processes (inorganic nutrient supply to the system) as well as the direct interaction between the plant and the herbivore and the plant and herbivore N : P ratios. In the context of species replacement, resource (nutrients) competition between plants can be mediated by herbivores and resource (plants) competition between herbivores is mediated by plants. This might lead to complex dynamics between plant and herbivore communities, with species replacement in which the plant nutrient limitation status can be under herbivore control or escape from this control, depending on the dominant species in the plant and herbivore communities. The dynamics might be different if the herbivores are specific or generalist grazers. Such mechanisms should be explored by both modelling and experiments. They might contribute to a better understanding of the cyclic plant–herbivore dynamics and species replacement commonly found in aquatic ecosystems.

Recent studies have shown that fishes in freshwater ecosystems can also play a stoichiometric role, not only by controlling zooplankton biomass and thus algal grazing, but also by stocking important quantities of N and P in constant ratios (Sterner & George 2000). Sterner's hypothesis has consequently to be revisited in a food-web context, and a model such as the one presented here could be extended to integrate several trophic levels.

Despite its simplicity, our model shows that, as far as ecological stoichiometry is concerned, intuitive arguments can hide complex mechanisms. A simple and general model like the one presented in this paper provides a good basis for a more rigorous reasoning, and may be useful to interpret more complex model behaviours or experimental results. It also shows that the stoichiometric approach can establish a link between direct and indirect interactions between trophic levels. Thus, stoichiometric constraints on essential elements such as N and P should be considered to better understand the dynamics of ecological systems.

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REFERENCES

- Amblard, C., Boisson, J.C., Bourdier, G., Fontvieille, D., Gayte, X. & Sime-Ngando, T. (1998). Ecologie microbienne en

- milieu aquatique: des virus aux protozoaires. *Revue des sciences de l'eau, numéro spécial*, 145–162.
- Andersen, T. (1997). Pelagic nutrient cycles, herbivores as sources and sinks. *Ecological Studies* 129. Springer-Verlag, Berlin, Germany.
- Andersen, T. & Hessen, D.O. (1991). Carbon, nitrogen, and phosphorus content of freshwater zooplankton. *Limnol. Oceanogr.*, 36, 807–814.
- Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A., & Thingstad, F. (1983). The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Series*, 10, 257–263.
- Burns, C.W. (1975). Differences in chemical composition between two species of *Daphnia* and some freshwater algae cultured in the laboratory. *Limnol. Oceanogr.*, 20, 1005–1011.
- Daufresne, T. & Loreau, M. (in press) Ecological stoichiometry, indirect interactions between primary producers and decomposers, and the persistence of ecosystems. *Ecology*.
- Downing, J.A. & Mccauley, E. (1992). The nitrogen: phosphorus relationship in lakes. *Limnol. Oceanogr.*, 37, 936–945.
- Elser, J.J., Dobberfuhl, D.R., Mackay, N.A. & Schampel, J.H. (1996). Organism size, life history, and N/P stoichiometry. Towards a unified view of cellular and ecosystem processes. *Bioscience*, 46, 674–684.
- Elser, J.J. & Urabe, J. (1999). The stoichiometry of consumer-driven nutrient recycling: theory, observations, and consequences. *Ecology*, 80, 735–751.
- Grover, J.P. (1997). resource competition. *Population and Community Biology*, Series 19. Chapman & Hall, London, U.K.
- Hecky, R.E. & Kilham, P. (1988). Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. *Limnol. Oceanogr.*, 33, 796–822.
- Hessen, D.O. (1990). Carbon, nitrogen and phosphorus status in *Daphnia* at varying food conditions. *J. Plankton Res.*, 12, 1239–1249.
- Hessen, D.O. (1992). Nutrient limitation of zooplankton production. *Am. Naturalist*, 140, 799–814.
- Hessen, D.O. (1997). Stoichiometry in food webs – Lotka revisited. *Oikos*, 79, 195–200.
- Hessen, D.O. & Andersen, T. (1992). The algae–grazer interface: feedback mechanisms linked to elemental ratios and nutrient cycling. *Arch. Hydrobiol. Beih.*, 35, 111–120.
- Hessen, D.O. & Lyche, A. (1991). Inter and intraspecific variation in zooplankton elemental composition. *Arch. Hydrobiol.*, 121, 343–353.
- Huxel, G.R. (1999). On the influence of food quality in consumer–resource interactions. *Ecol. Lett.*, 2, 256–261.
- Koski, M. (1999). Carbon: nitrogen ratios of Baltic Sea copepods – indication of mineral limitation? *J. Plankton Res.*, 21, 1565–1573.
- Lampert, W. (1986). Phytoplankton control by grazing zooplankton: a study on the spring clear-water phase. *Limnol. Oceanogr.*, 31, 478–490.
- Leibold, M.A. (1996). A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *Am. Naturalist*, 147, 784–812.
- Loreau, M. (1995). Consumers as maximizers of matter and energy flow in ecosystems. *Am. Naturalist*, 145, 22–42.
- Lotka, A.J. (1925). *Elements of Physical Biology*. Williams & Wilkins, Baltimore, U.S.A. Reprinted. 1956 as Lotka A. J., *Elements of Mathematical Biology*. Dover, New York, U.S.A.
- Olsen, Y., Jensen, A. Reinertsen, H., Borsheim, K.Y., Heldal, M. & Langeland, A. (1986). Dependence of the rate of release of phosphorus by zooplankton on the P:C ratio in food supply, as calculated by a recycling model. *Limnol. Oceanogr.*, 31, 34–44.
- Redfield, A.C. (1958). The biological control of chemical factors in the environment. *Am. Scientist.*, 46, 205–222.
- Reiners, W.A. (1986). Complementary models for ecosystems. *Am. Naturalist*, 127, 59–73.
- Rosswall, T. (1976). The internal nitrogen cycle between microorganisms, vegetation and soil, pp. 157–167. In: Svensson, B.H. & Söderlund, R., eds. *Nitrogen, Phosphorus and Sulphur – Global Cycles*. SCOPE Report 7, Stockholm: Ecological Bulletins.
- Rothhaupt, K.O. (1997). Grazing and nutrient influences of *Daphnia* and *Eudiaptomus* on phytoplankton in laboratory microcosms. *J. Plankton Res.*, 19, 125–139.
- Sterner, R.W. (1990). The ratio of nitrogen to phosphorus resupplied by herbivores: zooplankton and the algal competitive arena. *Am. Naturalist*, 136, 209–229.
- Sterner, R.W. (1993). *Daphnia* growth on varying quality of *Scenedesmus*. mineral limitation of zooplankton. *Limnol. Oceanogr.*, 38, 2351–2360.
- Sterner, R.W., Elser, J.J. & Hessen, D.O. (1992). Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems. *Biogeochemistry*, 17, 49–67.
- Sterner, W. & George, N.B. (2000). Carbon, nitrogen, and phosphorus stoichiometry of cyprinid fishes. *Ecology*, 81, 127–140.
- Sterner, R.W., Hagemeyer, D.D., Smith, W.L. & Smith, R.F. (1993). Phytoplankton nutrient limitation on food quality for *Daphnia*. *Limnol. Oceanogr.*, 38, 857–871.
- Tilman, D. (1982). Resource competition and community structure. Princeton University, Princeton, U.S.A.
- Urabe, J. (1993). N and P cycling coupled by grazers' activities: food quality and nutrient release by zooplankton. *Ecology*, 74, 2337–2350.
- Urabe, J. (1995). Direct and indirect effects of zooplankton on seston stoichiometry. *Ecoscience*, 2, 286–296.
- Urabe, J., Clasen, J. & Sterner, R.W. (1997). Phosphorus limitation of *Daphnia* growth: is it real? *Limnol. Oceanogr.*, 42, 1436–1443.
- Wetzel, R.G. (1983). *Limnology*. Saunders, London, U.K.

BIOSKETCH

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APPENDIX

Local stability analysis of nontrivial equilibria

Model without the herbivore

The model without the herbivore is obtained by setting N_h , P_h , H_N (N_p , N_h) and W_N (N_p , N_h) to zero in equation (1).

In this case, the model can lead to two feasible equilibria, one with the plant N limited, and the other with the plant P limited. Since these equilibria are symmetric, we arbitrarily present here the N limited equilibrium:

$$N_{il}^* = \frac{r_p + a}{n_N}; \quad N_p^* = S_N - N_{il}^*;$$

$$P_i^* = S_p - \frac{N_p^*}{\alpha}; \quad P_p^* = \alpha N_p^*.$$

Note that this equilibrium is feasible if and only if $N_p^* > 0$, i.e. $S_N > N_{il}^*$, and the condition for P limitation [inequality (9)] is not respected.

Stability analysis Since $N_p = \alpha P_p$, the model can be reduced to three independent variables: P_i , N_i , N_p . For more convenience (Loreau 1995), we substitute the variable N_T for N_i . N_T is the total amount of nitrogen contained in the system. The dynamic equation for N_T is:

$$\frac{dN_T}{dt} = a(S_N - N_T) \quad (A1)$$

with $N_T = S_N - N_i - N_p$.

The Jacobian matrix \mathbf{M} of the system is then:

$$\mathbf{M} = \begin{pmatrix} -a & -\frac{nN_p^*}{\alpha} & \frac{1}{\alpha}(n(N_p^* - N_i^*) + r_p) \\ 0 & -a & 0 \\ 0 & nN_p^* & -N_p^* \end{pmatrix}$$

Two of the three eigenvalues of \mathbf{M} equal $-a$, while the third equals $-N_p^*$. Thus, the three eigenvalues are always negative and the equilibrium is always locally stable when the feasibility condition is respected.

Model with donor-controlled herbivory

If the grazing function is donor-controlled, as in equation (16), the model can lead again to two feasible equilibria. Consider the case where the plant is N limited. At equilibrium:

$$N_{ilh}^* = \frac{r_p + a + b}{n}; \quad N_p^* = \left(\frac{\alpha}{\beta}\right)\left(\frac{n_h + a}{b}\right)N_h^*;$$

$$N_h^* = (S_N - N_i^*) \left(1 + \left(\frac{\beta}{\alpha}\right)\left(\frac{b}{n_h + a}\right)\right);$$

$$P_i^* = S_p - \frac{N_p^*}{\alpha} - \frac{N_h^*}{\beta}; \quad P_p^* = \alpha N_p^*; \quad P_h^* = \beta N_h^*.$$

This equilibrium is feasible if N_h^* is positive and if the condition for P limitation [inequality (9)] is not respected. *Stability analysis* Since $N_p = \alpha P_p$ and $N_h = \beta P_h$, the model can be reduced to four independent variables: P_i , N_i , N_p , P_p . The Jacobian matrix has two of its four eigenvalues equal to $-a$. The other two eigenvalues are the roots of the following equation:

$$a\lambda^2 + b\lambda + c = 0$$

with $a = 1$, $b = n_h + 2a + nN_p^*$ and

$$c = (nN_p^* + a)(n_h + a) + b\left(\frac{\beta}{\alpha}\right)nN_p^* \quad (A3)$$

Both are real and negative when the equilibrium is feasible ($N_p^* > 0$) because in this case a , b and c all are positive. Thus, provided the equilibrium is feasible, the four eigenvalues are always negative, and the equilibrium is always locally stable.

Model with Lotka–Volterra herbivory

In this case,

$$H_N(N_p, N_h) = b N_p N_h$$

The equilibrium values for the case of N limitation are:

$$N_{ilh}^* = \frac{r_p + a + bN_h^*}{n}; \quad N_p^* = \left(\frac{\alpha}{\beta}\right)\left(\frac{n_h + a}{b}\right);$$

$$N_h^* = \frac{S_N - \left[\left(\frac{r_p + a}{n}\right) + \left(\frac{r_h + a}{b}\right)\left(\frac{\alpha}{\beta}\right)\right]}{\left(1 + \frac{b}{n}\right)};$$

$$P_i^* = S_p - \frac{N_p^*}{\alpha} - \frac{N_h^*}{\beta}; \quad P_p^* = \alpha N_p^*; \quad P_h^* = \beta N_h^*.$$

As for the previous cases, two eigenvalues equal $-a$. The other two eigenvalues are the roots of equation (A3), with:

$$a = 1, b = nN_p^* \text{ and } c = b(n + b)\left(\frac{\beta}{\alpha}\right)N_h^*N_p^* \quad (A4)$$

Again both eigenvalues are real and always negative, and thus the equilibrium is always stable, when the equilibrium is feasible ($N_h^* > 0$ and $N_p^* > 0$).