

ECOLOGICAL STOICHIOMETRY, PRIMARY PRODUCER–DECOMPOSER INTERACTIONS, AND ECOSYSTEM PERSISTENCE

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Abstract. Primary producers and decomposers—the two most important groups for the functioning of ecosystems—have complex, indirect interactions. They are indirect mutualists through nutrient cycling, but also competitors for inorganic nutrients due to stoichiometric constraints in decomposers. We examine the conditions under which they are able to coexist, and hence ecosystems are able to persist, using a stoichiometrically explicit minimum model for an ecosystem. The model takes into account the coupling of carbon and a nutrient in the biomass and detritus, the nutrient limitation and the energy-providing role of primary producers, the recycling role of decomposers, and the stoichiometric constraints leading to indirect competition for the nutrient. The model shows that two conditions must be met to ensure coexistence of primary producers and decomposers: (1) decomposers must be limited by the carbon provided by plant detritus, and (2) the difference between the carbon : nutrient ratios of primary producers and decomposers must be sufficiently small. Condition (1) is fulfilled if decomposers are better competitors than primary producers for nutrient uptake. When nutrient uptake by plants and decomposers has a Lotka-Volterra form, these results are robust whether the nutrient cycle is closed or open. When nutrient uptake is donor controlled, however, coexistence is facilitated by an open nutrient cycle. We conclude that ecosystem persistence is not a trivial issue when stoichiometry is taken into account in ecological processes. Strict conditions on the carbon : nutrient ratios and competitive abilities of plants and microorganisms may be required. Given these theoretical results, we highlight the lack of experimental data concerning primary producer and decomposer coexistence conditions, and we suggest that more research has to be performed.

Key words: carbon cycle; decomposition; ecosystem persistence; immobilization; indirect interactions; nutrient cycles; stoichiometry.

INTRODUCTION

Decomposers play a key role in the primary productivity of ecosystems through their contribution to the recycling of essential chemical elements (Fig. 1) such as nitrogen or phosphorus that are in limited supply for primary producers (Rosswall 1976, Bosatta and Berendse 1984, Vitousek and Matson 1985, Hunt et al. 1988, Harte and Kinzig 1993). Paradoxically, though, decomposers (more specifically, bacteria) are known to compete with primary producers for the uptake of those limiting nutrients. Such a competition is a consequence of stoichiometry on carbon and nutrients in the transfer of matter between primary producers and decomposers. Indeed, the carbon : nutrient ratio of primary producers is usually larger than that of decomposers (Ågren and Bosatta 1996). Despite this mismatch, decomposers maintain homeostasis in terms of carbon and nutrient content when they feed on an inadequate resource (Ågren and Bosatta 1996). In order to do this, they employ another source of the deficient nutrient, most of the time the free nutrient pool available to primary producers (Bosatta and Berendse 1984). This process

is called “immobilization” (Fig. 1), and occurs in both terrestrial and aquatic ecosystems. This uptake of nutrient by decomposers is usually just a stage in the decomposition process, which leads ultimately to the net mineralization of the substrate nutrient content (mineralization minus immobilization, see Fig. 1) and the final release of the immobilized nutrient (Ågren and Bosatta 1996). Because of this immobilization process, however, decomposers compete with primary producers for nutrient uptake (Currie and Kalf 1984, Jackson et al. 1989, Schimel et al. 1989, Jingguo and Bakken 1997, Kaye and Hart 1997). Therefore, primary producers and decomposers are linked by both indirect competitive and mutualistic interactions (Fig. 1): they compete for the same nutrient, but primary producers need decomposers for nutrient recycling and heterotrophic decomposers need primary producers for their energy supply (Cole et al. 1984, Baines and Pace 1991).

From a theoretical point of view, Lotka (1925) was among the first to notice the general importance of homeostasis in the functioning of food webs. Several theoretical studies have recently dealt with homeostasis maintenance and its implication for ecosystem functioning. Such studies are now increasingly combined with “ecological stoichiometry,” defined by Elser and Urabe (1999) as “an approach that analyzes the constraints and consequences of mass balance of multiple

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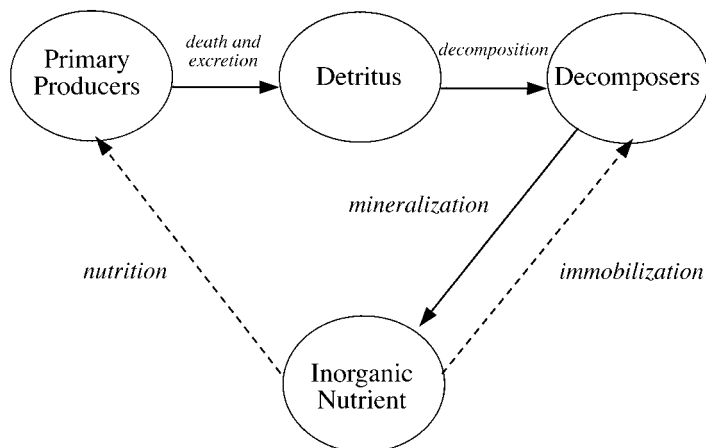


FIG. 1. Indirect mutualism and resource competition in a primary producer-decomposer system with nutrient recycling. Arrows represent matter transfers. Continuous arrows mediate indirect mutualistic interactions: the primary producers provide detritus through death and excretion, which constitutes the energy resource for decomposers. Decomposers consume the detritus (decomposition) and recycle the nutrient by mineralization. Dotted arrows mediate resource competition: primary producers take up the nutrient for their growth (nutrition), and decomposers "immobilize" the nutrient (immobilization) to maintain a lower carbon:nutrient ratio than that of primary producers.

chemical elements in ecological interactions." Most of them have focused on primary producer-herbivore relations (Sternner 1990, Hessen 1997). Few have addressed relations between primary producers and decomposers, taking into account C:N coupling and decomposers C/N limitation (Ågren and Bosatta 1996, Thingstad and Lignell 1997, Thingstad et al. 1999).

Explicit consideration of the mixing of positive and negative interactions between primary producers and decomposers raises questions regarding the coexistence of these two functional groups. Bratbak and Thingstad (1985) considered this as a paradox of competition and commensalism in aquatic ecosystems, but they did not explicitly take into account the recycling role of decomposers in their work. It is generally admitted that primary producers are nutrient limited in many ecosystems (Gutschick 1981, DeAngelis 1992, Tanner et al. 1998), but there is little consensus regarding the nutrient status and limitation of decomposers. Many field studies concluded that decomposers feeding on primary producer detritus are carbon limited, i.e., the inorganic nutrient stock is sufficient for immobilization and decomposer growth is limited by the stock of available detritus (Bird and Kalff 1984, Vadstein et al. 1989, Kirchman and Richard 1990). However, other studies found that decomposers are nutrient limited, i.e., the inorganic nutrient stock is not sufficient to cover the needs of decomposers and thus limits decomposer growth, especially in aquatic ecosystems (Morris and William 1992, Thingstad et al. 1998, Zohary and Roberts 1998). The latter conclusion seems to contradict the competitive exclusion principle since the two groups would coexist on the same limiting resource (Tilman 1982). On considering the case of freshwater algae and heterotrophic bacteria competing for phosphorus, Currie and Kalff (1984) formulated the carbon limitation hypothesis. They claimed that the persistence of the system demands that bacteria should always be competitive enough for nutrients to be limited

by the supply of organic carbon provided by algae rather than by the inorganic nutrient pool. In this manner, competitive exclusion would not occur.

On the other hand, those theoretical studies that have explicitly considered recycling have not considered the potential competitive interaction between primary producers and decomposers (Pastor and Post 1986, Parton et al. 1993, Loreau 1994, 1998, McKane et al. 1997). If one considers that in many ecosystems cycles of limiting nutrients generally tend to become increasingly closed as succession proceeds (Odum 1969, Loreau 1998) and nutrient immobilization fluxes are quantitatively important, a good understanding of primary producer-decomposer systems and ecosystem persistence in general requires consideration of all the indirect interactions occurring between these organisms.

These considerations suggest that the coexistence of primary producers and decomposers, and the carbon limitation hypothesis formulated by Currie and Kalff (1984), should be revisited in the context of nutrient recycling and stoichiometry.

In this paper, we address the problem of the coexistence of primary producers and decomposers, taking into account the energy-providing role of primary producers, the recycling role of decomposers, and the stoichiometric constraints leading to indirect competition for a limiting nutrient. We propose a theoretical approach to the problem in which (1) we explore the carbon limitation hypothesis (Currie and Kalff 1984) when nutrient cycling is taken into account, i.e., we examine whether a primary producer-decomposer system mixing indirect mutualism and indirect competition for the same nutrient is able to persist only if decomposers are "carbon limited"; and (2) we explore the roles of the competitive ability and carbon:nutrient ratio of both protagonists for the persistence of this system.

To this end, we first present and analyze a simple model for primary producers-decomposers systems.

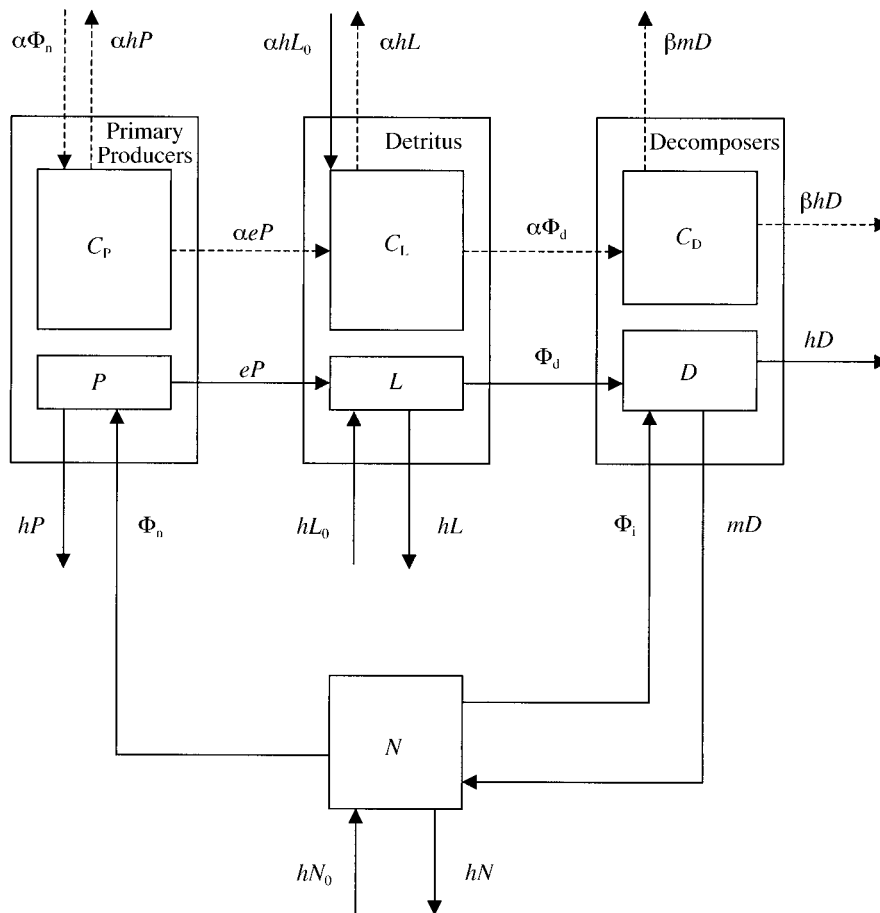


FIG. 2. Flow diagram of the general compartment model coupling carbon and one limiting nutrient in a primary producer-decomposer system. N , P , L , and D represent the inorganic nutrient, the nutrient stocks in the primary producer biomass, detritus, and decomposer biomass, respectively. C_p , C_L , and C_D represent the carbon stocks in the primary producer biomass, detritus, and decomposer biomass, respectively. The arrows represent the nutrient (continuous arrows) and carbon (dashed arrows) flows between compartments. The expressions Φ_n and $\alpha\Phi_n$ are the nutrient and carbon flows, respectively, associated with nutrition and net photosynthesis by primary producers; eP and αeP are the nutrient and carbon flows associated with death and excretion of primary producers; Φ_d and $\alpha\Phi_d$ are the nutrient and carbon flows associated with the decomposition of detritus by decomposers; mD and βmD are the nutrient and carbon flows associated with nutrient mineralization and heterotrophic respiration; Φ_i is the nutrient flow associated with nutrient immobilisation; hP and αhP , hL and αhL , hD and βhD , and hN_0 and hN represent the nutrient and carbon flows associated with the dilution rate of the system; and hL_0 and αhL_0 represent the nutrient and carbon input to the detritus pool from allochthonous sources of organic matter associated with the dilution rate of the system.

The model is stoichiometrically explicit in the sense of Elser et al. (1996), and combines indirect mutualism and competition generated by stoichiometric constraints on carbon and an essential nutrient limiting primary production. We then explore the robustness of the results to different forms of competition and to the opening of the nutrient cycle.

THE GENERAL MODEL

We present here a simple and general compartment model of a primary producer-decomposer system that couples the cycles of carbon (C) and a limiting nutrient (N). This system represents a minimum ecosystem in terms of functioning, because primary producers syn-

thesize biomass and decomposers allow nutrient cycling by their capacity to mineralize the biomass. Compartment models are appropriate for modeling stoichiometry and element cycling in ecosystems because they allow explicit consideration of mass-balance constraints for each element and explicit information on the relations between physiological coupling constraints and recycling processes.

The model (Fig. 2) is made up of three carbon compartments coupled with three nutrient compartments by constant C:N ratios, plus one free nutrient compartment. The primary producer community takes up nutrient (flux Φ_n on Fig. 2) and carbon (flux $\alpha\Phi_n$ on Fig. 2) from inorganic sources, and combines these two el-

elements into its own biomass at a constant C:N ratio, α . Death and excretion of organic matter from primary producers (fluxes eP and αeP on Fig. 2) generate a pool of dead organic matter that we call "detritus" in this paper. We assume that the fluxes of nutrient and carbon associated with this flux of organic matter are combined in the same ratio, α , as that of primary producer biomass. This assumption underestimates the C:N ratio of the detritus; excreta and even dead organic matter are usually less concentrated in nutrient than is the primary producer biomass, but such an assumption simplifies the analysis of the model considerably without changing the results qualitatively.

The detritus is a substrate for the decomposer community whose C:N ratio β is constant and smaller than α (Ågren and Bosatta 1996, Andersen 1997). Decomposers consume the organic matter of detritus (fluxes Φ_d and $\alpha\Phi_d$ on Fig. 2) and mineralize the nutrient (flux mD on Fig. 2) and carbon (flux βmD on Fig. 2), ending the coupling between these two elements in the organic matter. Due to the difference between α and β , the maintenance of decomposer homeostasis entails an immobilization flux (flux Φ_i on Fig. 2) associated with the decomposition flux and proportional to the difference between α and β .

Let us define variables P and C_p as the amounts of nutrient and carbon, respectively, contained in the primary producer compartment, L and C_L as the amounts of nutrient and carbon, respectively, contained in the detritus compartment, D and C_D as the amounts of nutrient and carbon, respectively, contained in the decomposer compartment, and N as the amount of nutrient available in inorganic form. The dynamical equations for the model are obtained by setting the time derivative of the variables equal to the sum of inflows minus the sum of outflows for each compartment:

$$\begin{aligned}\dot{P} &= \Phi_n - (e + h)P \\ \dot{C}_p &= \alpha(\Phi_n - (e + h)P) \\ \dot{L} &= eP + hL_0 - \Phi_d - hL \\ \dot{C}_L &= \alpha(eP + hL_0 - \Phi_d - hL) \\ \dot{D} &= \Phi_i + \Phi_d - (m + h)D \\ \dot{C}_D &= \alpha\Phi_d - \beta(m + h)D \\ \dot{N} &= hN_0 + mD - hN - \Phi_i - \Phi_n\end{aligned}\quad (1)$$

where dots on variables denote time derivatives.

The functions $\Phi_n(N, P)$, $\Phi_d(N, D, L)$, and $\Phi_i(N, D, L)$ represent the nutrition flux, decomposition flux, and immobilization flux, respectively. The functional forms of Φ_n , Φ_d , and Φ_i will vary with the different applications of the general model, and thus will be specified later. For the sake of simplicity, the system is of a chemostat type, with a constant dilution rate h and a constant inflowing amount of nutrient N_0 and allochthonous detritus L_0 . Primary producer growth is as-

sumed to be always limited by the inorganic nutrient pool N ; the excretion and mineralization fluxes of the nutrient are donor controlled with excretion rate e and mineralization rate m , respectively.

The maintenance of primary producer, detritus, and decomposer homeostasis is provided by the following conditions:

$$\dot{C}_p = \alpha\dot{P}\quad (2)$$

$$\dot{C}_L = \alpha\dot{L}\quad (3)$$

$$\dot{C}_D = \beta\dot{D}\quad (4)$$

Eq. 2 refers to the assumption that primary producers control their carbon:nutrient ratio by adjusting their carbon input so that the net photosynthesis flux is equal to $\alpha\Phi_n$, and Eq. 3, that the ratio stays constant during the transfer of biomass to the detritus and the decomposers. Eq. 4 constrains the relationship between the decomposition flux Φ_d and the immobilization flux Φ_i . Using Eq. 1 leads to the constraint

$$\Phi_i = \left(\frac{\alpha - \beta}{\beta}\right)\Phi_d.\quad (5)$$

Because of this strict carbon and nutrient coupling in the living and nonliving organic matter stocks and fluxes, we may reduce the model to four independent variables, the stocks of either carbon or nutrient in the primary producer, detritus, and decomposer compartments, and the inorganic nutrient pool. We have arbitrarily chosen the nutrient stocks to measure biomass. Thus, Eq. 1 can be reduced to

$$\begin{aligned}\dot{P} &= \Phi_n - (e + h)P \\ \dot{L} &= eP + hL_0 - \Phi_d - hL \\ \dot{D} &= \Phi_i + \Phi_d - (m + h)D \\ \dot{N} &= hN_0 + mD - hN - \Phi_i - \Phi_n.\end{aligned}\quad (6)$$

Decomposer growth can be either carbon or nutrient limited. By "carbon limited" we mean that decomposer growth is limited by the amount of carbon in the detritus pool, L , available for decomposition. In this case, the inorganic nutrient stock, N , is large enough so that the immobilization flux, Φ_i , is sufficient to compensate for the lack of nutrient entailed by the detritus decomposition flux, Φ_d . By "nutrient limited" we mean that decomposer growth is limited by the availability of the inorganic nutrient, N . In this case, N is not large enough and Φ_i is not sufficient to compensate for the lack of nutrient entailed by Φ_d , so that Φ_i limits decomposer growth and hence the decomposition, Φ_d , of the detritus.

Under carbon limitation, the decomposition flux, Φ_d , is expressed by a donor-controlled function, dL , where d is the decomposition rate under carbon limitation. In this case the immobilization flux, Φ_i , compensates for the lack of nutrient, and thus this flux is driven by the decomposition flux. According to Eq. 5,

TABLE 1. Summary of symbols.

Symbols	Explanation	Dimension
Variables		
P	nutrient stock in primary producer biomass	quantity of nutrient
L	nutrient stock in detritus	quantity of nutrient
D	nutrient stock in decomposer biomass	quantity of nutrient
N	free nutrient stock	quantity of nutrient
Parameters		
N_T	total amount of nutrient in the system	quantity of nutrient
n	primary producer nutrition rate (LVC and LVO models)	(time) ⁻¹ ·(quantity of nutrient) ⁻¹
i	immobilization rate (LVC and LVO models)	(time) ⁻¹ ·(quantity of nutrient) ⁻¹
n'	primary producer nutrition rate (DCC and DCO models)	(time) ⁻¹
i'	immobilization rate (DCC and DCO models)	(time) ⁻¹
e	death and excretion rate of primary producers	(time) ⁻¹
d	detritus decomposition rate when decomposers are carbon limited	(time) ⁻¹
m	mineralization rate	(time) ⁻¹
α	carbon : nutrient ratio in primary producer biomass and detritus (LVC, LVO, DCC, DCO models)	dimensionless
β	carbon : nutrient ratio in decomposer biomass	dimensionless
functions		
Φ_n	nutrient flux associated with nutrition	(quantity of nutrient)·(time) ⁻¹
Φ_d	nutrient flux associated with decomposition	(quantity of nutrient)·(time) ⁻¹
Φ_i	nutrient flux associated with immobilization	(quantity of nutrient)·(time) ⁻¹

$$\Phi_i = \left(\frac{\alpha - \beta}{\beta} \right) \Phi_d = \left(\frac{\alpha - \beta}{\beta} \right) dL. \quad (7)$$

Under nutrient limitation, the decomposition flux is controlled by the immobilization flux. In this case, the immobilization flux $\Phi_i = g(N, D)$. Thus, according to Eq. 5,

$$\Phi_d = \left(\frac{\beta}{\alpha - \beta} \right) \Phi_i = \left(\frac{\beta}{\alpha - \beta} \right) g(N, D). \quad (8)$$

Liebig's law of the minimum determines whether decomposers are carbon or nutrient limited. We express Liebig's law in the simplest way, using a minimum function (Grover 1997), so that

$$\Phi_i = \min \left[g(N, D); \left(\frac{\alpha - \beta}{\beta} \right) dL \right] \quad (9)$$

$$\Phi_d = \min \left[\left(\frac{\beta}{\alpha - \beta} \right) g(N, D); dL \right]. \quad (10)$$

Switching between carbon or nutrient limitation in decomposers is then determined by a threshold value, g_{lim} , of the immobilization function $g(N, D)$, defined as follows:

$$g_{\text{lim}} = \left(\frac{\alpha - \beta}{\beta} \right) dL. \quad (11)$$

If $g(N, D) > g_{\text{lim}}$, decomposer growth is carbon limited. Alternatively, if $g(N, D) < g_{\text{lim}}$, decomposer growth is nutrient limited.

THE SPECIFIC APPLICATIONS OF THE GENERAL MODEL

We address the questions of primary producer and decomposer coexistence and ecosystem persistence by

analyzing four different applications of the general model. These applications differ in the functions chosen for the nutrition and immobilization fluxes when decomposers are nutrient limited, and in the degree of closure of the system in terms of nutrient.

The first application (the Lotka-Volterra closed model) is an extreme case of a closed ecosystem with Lotka-Volterra functions for nutrient uptake by both the primary producers and decomposers. This case highlights the indirect interactions (both competitive and mutualistic) between primary producers and decomposers, since (1) Lotka-Volterra trophic functions classically lead to competitive exclusion of one of the protagonists (Grover 1997), and thus the carbon limitation hypothesis should be verified, and (2) nutrient availability for primary producers relies entirely on the recycling process in a closed ecosystem.

The other three applications aim at testing the robustness of the results obtained with the Lotka-Volterra closed model under less restrictive conditions. The models and results for each scenario are detailed in the following sections. All the parameters are summarized in Table 1.

The Lotka-Volterra closed model (LVC)

The LVC model is characterized by nutrient consumption functions of a Lotka-Volterra type for both primary producers and decomposers when the latter are nutrient limited. We use here the simplest formalism for Lotka-Volterra functions, but forms that are more realistic could be used (Bratbak and Thingstad 1985), probably without changing the main conclusions. Thus, the nutrition flux is $\Phi_n = nPN$, where n is the nutrition rate, and the immobilization flux when decomposers are nutrient limited is $\Phi_i = g(N, D) = iDN$, where i is

the immobilization rate. The closure of the system is obtained by setting the dilution rate to zero ($h = 0$). Because of this closure, the total amount of nutrient in the system, N_T , is conserved, and one of the variables can be expressed as a linear combination of the other variables:

$$N = N_T - P - L - D. \quad (12)$$

The LVC model then reduces to three dynamical equations:

$$\begin{aligned} \dot{P} &= nPN - eP \\ \dot{L} &= eP - \min\left[\left(\frac{\beta}{\alpha - \beta}\right)iDN; dL\right] \\ \dot{D} &= \min\left[\left(\frac{\alpha}{\alpha - \beta}\right)iDN; \left(\frac{\alpha}{\beta}\right)dL\right] - mD \end{aligned} \quad (13)$$

where Eq. 12 holds.

We present here the main results of the analysis of this model. More details are provided in Appendix A. At steady state, the time derivatives in Eq. 13 are equal to zero. Solving these equations provides the steady-state nutrient stocks in primary producers (P^*), detritus (L^*), decomposers (D^*), and inorganic nutrient pool (N^*) for the two types of decomposer limitation.

When decomposers are carbon limited, the system can reach two steady states: (1) a trivial steady state

$$P^* = 0, L^* = 0, D^* = 0, N^* = N_T \quad (14)$$

and (2) a nontrivial steady state:

$$\begin{aligned} P^* &= \frac{N_T - N^*}{1 + \frac{e}{d} + \frac{\alpha e}{\beta m}} & L^* &= \left(\frac{e}{d}\right)P^* \\ D^* &= \left(\frac{\alpha e}{\beta m}\right)P^* & N^* &= \frac{e}{n}. \end{aligned} \quad (15)$$

Under carbon limitation, the system persists at steady state when it reaches Eq. 15 with positive values for P^* , L^* , and D^* , i.e., the total amount of detritus is sufficient ($N_T > e/n$). In this case, primary producers control the inorganic nutrient pool. This is consistent with the traditional approach of resource competition between primary producers in a homogeneous environment (Tilman 1982, Grover 1997, Loreau 1998).

When decomposers are nutrient limited, the system can reach an infinity of steady states, but with primary producers (P^*) and decomposers (D^*) both absent, and all the nutrient being stocked into the detritus (L^*) and inorganic nutrient (N^*) compartments

$$\begin{aligned} P^* &= 0 & L^* &= aN_T \\ D^* &= 0 & N^* &= bN_T \end{aligned} \quad (16)$$

with

$$a + b = 1.$$

Thus, the steady state under nutrient limitation of decomposers is a collapse of the ecosystem.

Considering the steady states described by Eqs. 14–16, notice that primary producers and decomposers coexist at steady state if and only if the system of equations in Eq. 15 is stable and feasible. Thus, the stability and feasibility conditions for Eq. 15 are the conditions for the persistence of the system.

The feasibility of a steady state is defined here by the consistency between the immobilization function at steady state, iD^*N^* , and the threshold value g_{lim} determining switching between carbon and nutrient limitations as defined in Eq. 11. In the case of decomposer carbon limitation, a steady state is feasible if the immobilization function $iD^*N^* > g_{\text{lim}}$. If it is smaller than this threshold, it means that decomposers are effectively nutrient limited, and the steady state has no biological meaning. In the case of decomposer nutrient limitation, the reverse is true: the immobilization function iD^*N^* must be $< g_{\text{lim}}$ for the steady state to be feasible.

According to Routh-Hurwitz criteria (May 1974), the conditions for the local stability of the coexistence steady state described in Eq. 15 are the following: (1) The total amount of nutrient contained in the system must be greater than the minimum value that allows persistence of the primary producers ($N_T > e/n$). (2) The ratio of mineralization rate m to death and excretion rate e must be large enough compared with the ratio of α to β (see condition A1.7 in Appendix A). If this second condition is not fulfilled, stability is not granted, and requires more complex conditions that are presented in Appendix A. These conditions have much more chance to be satisfied if the ratio of α to β is small.

These results are important because they show that, even when producers and decomposers are limited by different nutrients (primary producers are nutrient limited and decomposers are carbon limited), their coexistence may not be a trivial issue. The second condition mentioned in the last paragraph results from the stoichiometric constraints on carbon and nutrient which entail the immobilization process. Indeed, if primary producers and decomposers have the same carbon : nutrient ratio (i.e., $\alpha = \beta$), the immobilization process does not occur and the only condition required for the stability of the coexistence steady state described in Eq. 15 is the first condition mentioned in the last paragraph (Appendix A).

The condition for the feasibility of the steady state described by Eq. 15 is determined by the relative competitive abilities of primary producers and decomposers for nutrient uptake, namely n/e and $i/m[\alpha/(\alpha - \beta)]$ (Appendix A). The steady state described in Eq. 15 is feasible if decomposers have the competitive superiority:

$$\frac{i}{m} \left(\frac{\alpha}{\alpha - \beta} \right) > \frac{n}{e}. \quad (17)$$

Thus, when the conditions for the stability of the steady state described in Eq. 15 are fulfilled, the carbon hypothesis is respected and the competitive abilities of the two protagonists determine the fate of the ecosystem.

When primary producers have the competitive superiority for nutrient uptake, i.e., when

$$\frac{n}{e} > \frac{i}{m} \left(\frac{\alpha}{\alpha - \beta} \right) \quad (18)$$

competitive exclusion occurs, leading to the disappearance of decomposers. The mineralization process is stopped, and primary producers empty the inorganic pool of nutrient. Primary producers eventually disappear, and the total amount of nutrient in the system is stocked into the detritus compartment: the steady state described in Eq. 15 is reached, with $a = 0$ and $b = 1$, hence $L^* = N_T$. Thus, coexistence between primary producers and decomposers is impossible, and the ecosystem collapses.

When decomposers have the competitive superiority for nutrient uptake, i.e., when the condition described in Eq. 17 is met, they have the capacity to exclude primary producers. However, competitive exclusion does not occur because decomposers switch to carbon limitation: the steady state described in Eq. 15 is reached. Thus, primary producers and decomposers coexist, and the ecosystem persists.

Thus, our results show, first, that the carbon limitation hypothesis is verified for the LVC model, i.e., primary producers and decomposers are able to coexist at steady state only if decomposers are carbon limited. Second, they show that carbon limitation at steady state for decomposers does not necessarily imply coexistence, and that coexistence depends on strict conditions entailed by the stoichiometric constraints on carbon and the nutrient. Third, they show that carbon limitation for decomposers at steady state depends on their competitive ability for nutrient uptake. This competitive ability itself depends on the stoichiometric constraints on carbon and the nutrient, and more precisely the difference between the carbon:nutrient ratio in primary producer and decomposer biomass.

Robustness to donor-controlled interactions: the donor-controlled closed model (DCC)

As primary producers and decomposers often coexist and compete for nutrients in heterogeneous environments, especially in terrestrial ecosystems (Jingguo and Bakken 1997), one could argue that a Lotka-Volterra type competition is an unrealistic formalism, because heterogeneity prevents large-scale control of the resource by the consumers (Smith 1972, Strong 1992). To examine the robustness of our model to the type of control of the consumer-resource interaction, we consider another extreme situation where none of the protagonists controls the level of inorganic nutrient, and we use simple donor-controlled functions as a conve-

nient expression for the nutrition flux and the immobilization flux when decomposers are nutrient limited. Such functions do not lead to competitive exclusion in classical competition situations without indirect mutualistic interactions, and their simplicity allow us to perform an analytical study of the model.

The DCC model differs from the LVC model only by the donor-controlled form of resource consumption by primary producers and decomposers. The nutrition flux is now $\Phi_n = n'N$, where n' is the nutrition rate, and the immobilization flux when decomposers are nutrient limited is $\Phi_i = g(N) = i'N$, where i' is the immobilization rate. As in the LVC model, the ecosystem is assumed to be closed, the dilution rate being zero ($h = 0$).

Since the model is linear, there is only one steady state per type of decomposer limitation. (1) When decomposers are carbon limited,

$$\begin{aligned} P^* &= \frac{N_T}{\chi^1} & L^* &= \frac{e}{d} P^* \\ D^* &= \left(\frac{\alpha e}{\beta m} \right) P^* & N^* &= \frac{e}{n'} P^* \end{aligned} \quad (19)$$

with

$$\chi^1 = 1 + \frac{e}{n'} + \frac{e}{d} + \frac{\alpha e}{\beta m}.$$

(2) When decomposers are nutrient limited,

$$\begin{aligned} P^* &= 0 & L^* &= N_T \\ D^* &= 0 & N^* &= 0. \end{aligned} \quad (20)$$

Despite some differences in the steady states, the outcomes are qualitatively similar to those of the LVC model: the steady state under nutrient limitation of the decomposers is a collapse of the ecosystem, whereas the ecosystem persists under carbon limitation. Thus, the conditions for ecosystem persistence are those for the stability and feasibility of the steady state described in the system of equations in Eq. 19.

The stability analysis of the steady state described in Eq. 19 is detailed in Appendix B. As in Eq. 15, the stability of the system in Eq. 19 depends on conditions that involve the stoichiometric constraints on carbon and nutrient. The lower α compared to β , and the higher the mineralization rate m , the more stability is facilitated.

We assessed the feasibility of the steady state described in Eq. 19 in the same manner as for Eq. 15 (Appendix B). The feasibility condition is

$$i' \left(\frac{\beta}{\alpha - \beta} \right) > n'. \quad (21)$$

Thus, as for the LVC model, when the stability conditions are fulfilled, the carbon hypothesis is respected. For this model, since competition for nutrient is expressed by donor-controlled functions, one may con-

sider the nutrition rate n' and immobilization rate i' as measures of competitive abilities for nutrient uptake.

When the decomposer immobilization rate i' is sufficiently small compared with the primary producer nutrition rate n' , i.e.,

$$i' \left(\frac{\beta}{\alpha - \beta} \right) < n' \quad (22)$$

then decomposers become nutrient limited and disappear. The steady state described in Eq. 20 is then reached, with all the nutrient trapped in detritus. Thus, coexistence is impossible and the ecosystem collapses.

When the decomposer immobilization rate i' is sufficiently large compared with the primary producer nutrition rate n' , i.e., the condition described in Eq. 21 is respected, decomposers are maintained under carbon limitation, and the steady state described in Eq. 19 is reached. Thus, primary producers and decomposers coexist and the ecosystem persists.

Notice the similarities with the LVC model. Even though competitive exclusion should not occur in this linear model, ecosystem persistence also depends on conditions including the competitive abilities of primary producers and decomposers (more precisely, the immobilization rate i' and the nutrition rate n'), the difference between the ratios α and β , and the mineralization rate m . However, the reasons leading to ecosystem collapse when decomposers are nutrient limited are different. In the DCC model, when decomposers are nutrient limited, the amount of nutrient in the inorganic pool N controls the nutrition and immobilization fluxes, and hence indirectly controls all the other fluxes in the system, which are proportional to N . As a consequence, a steady state can only be reached when $N = 0$, and it is stable only if the input to the detritus compartment is larger than its output, i.e., when the nutrition flux $\Phi_n = n'N$ is larger than the decomposition flux $\Phi_d = [\beta/(\alpha - \beta)]i'N$. This leads to the condition described in Eq. 22. On the contrary, if this condition is not met (i.e., if the condition described in Eq. 21 holds), this steady state is not stable, and the detritus L always decreases, whereas D and N increase. This situation eventually leads to carbon limitation for the decomposers, and consequently to the persistent steady state, which is feasible in this case. Note that this behavior is due to the closure of the system, which forces the detritus to be a sink when the condition described in Eq. 22 is met.

Since the general results obtained with the DCC model are similar to those of the LVC model, we conclude that in a closed system, the carbon limitation hypothesis is verified even though competitive exclusion does not occur. However, the similarity of the two model behaviors hides different properties, in particular with regard to the opening of the system.

Robustness to the opening of the nutrient cycle: the Lotka-Volterra open (LVO) and donor-controlled open (DCO) models

We restricted the analysis to a closed nutrient cycle in the two previous applications by setting the dilution rate h equal to zero. The closure of the ecosystem implied an obligatory indirect mutualism between primary producers and decomposers because mineralization is then the only source of inorganic nutrient for primary producers. In reality, few ecosystems are strictly closed with respect to nutrients. Thus it seems interesting to test the robustness of our previous results to the opening of the nutrient cycle, all the more so since those of the DCC model seem to depend on the closure of the ecosystem. Here we revisit the LVC and DCC models, but with a nonzero dilution rate h . In order to keep consistency with LVC and DCC in terms of organic carbon cycle, we set the allochthonous source of detritus L_0 to 0. The two applications thus obtained are called the Lotka-Volterra open (LVO) and the donor-controlled open (DCO) model, respectively. The dynamical equations for these models are obtained from the set of Eqs. 6, with the nutrition, decomposition, and immobilization fluxes defined as in the LVC or DCC model, respectively. The nontrivial steady states feasible for C and N limited decomposers are presented in Table 2.

Concerning the LVO model, note that for C-limited decomposers the steady state is similar to that of LVC, except for the presence of the dilution rate h in the equations (Table 2). On the other hand, for N-limited decomposers, primary producers and decomposers can persist separately because the mutualistic interaction is not obligatory. However, we have to reject the steady state where primary producer are excluded and decomposers survive alone because it has no biological meaning since D and L have opposite signs. This is the consequence of nutrient-driven decomposition becoming unrealistic when primary producers disappear and stop to provide detritus.

Considering the stability and feasibility conditions of the steady states, one can easily show that the carbon hypothesis is respected in the same way as for the LVC model.

When the primary producers have the competitive superiority for nutrient uptake, i.e.,

$$\frac{n}{e + h} > \left(\frac{i}{m + h} \right) \left(\frac{\alpha}{\alpha - \beta} \right) \quad (23)$$

then competitive exclusion occurs, leading to the disappearance of decomposers. The mineralization process is stopped but the primary producers can survive without nutrient recycling because of the constant input of nutrient hN_0 into the system. Then the decomposer exclusion is reached. This situation is comparable to intensive methods of cultivation where primary production is only sustained by nutrient input. Obviously,

TABLE 2. Nontrivial feasible steady states for the four applications of the model, when decomposers are C-limited or N-limited.

Decomposer type	Model			
	LVC	DCC	LVO	DCO
C-limited	coexistence	coexistence	coexistence	coexistence
	$P^* = \frac{N_T - N^*}{1 + \frac{e}{d} + \frac{\alpha e}{\beta m}}$	$P^* = \frac{N_T}{\chi^1}$	$P^* = \frac{N_0 - N^*}{1 + \frac{e}{(d+h)} + \frac{\alpha de}{\beta(d+h)(m+h)}}$	$P^* = \frac{N_0}{\chi^2}$
	$L^* = \left(\frac{e}{d}\right)P^*$	$L^* = \left(\frac{e}{d}\right)P^*$	$L^* = \left(\frac{e}{(d+h)}\right)P^*$	$L^* = \left(\frac{e}{(d+h)}\right)P^*$
	$D^* = \left(\frac{\alpha e}{\beta m}\right)P^*$	$D^* = \left(\frac{\alpha e}{\beta m}\right)P^*$	$D^* = \left(\frac{\alpha ed}{\beta(m+h)(d+h)}\right)P^*$	$D^* = \left(\frac{\alpha ed}{\beta(m+h)(d+h)}\right)P^*$
	$N^* = \frac{e}{n}$	$N^* = \left(\frac{e}{n'}\right)P^*$	$N^* = \frac{(e+h)}{n}$	$N^* = \left(\frac{(e+h)}{n'}\right)P^*$
N-limited	collapse	collapse	decomposers excluded	coexistence
	$P^* = 0$	$P^* = 0$	$P^* = \frac{h}{e+h}(N_0 - N^*)$	$P^* = \frac{N_0}{\chi^3}$
	$L^* = aN_T$	$L^* = N_T$	$L^* = \left(\frac{e}{h}\right)P^*$	$L^* = \left(\frac{e - \frac{\beta(e+h)i'}{(\alpha-\beta)}}{n'h}\right)P^*$
	$D^* = 0$	$D^* = 0$	$D^* = 0$	$D^* = \left(\frac{\alpha i'(e+h)}{(\alpha-\beta)(m+h)n'}\right)P^*$
	$N^* = bN_T$ with $a + b = 1$	$N^* = 0$	$N^* = \frac{e+h}{n}$	$N^* = \left(\frac{(e+h)}{n'}\right)P^*$
			or primary producers excluded	
			$P^* = 0$	
			$L^* = -\left(\frac{iN^*D^*}{h}\right)\left(\frac{\beta}{\alpha-\beta}\right)$	
			$D^* = \frac{h(N^* - N_0)}{h - \left(\frac{\beta}{\alpha-\beta}\right)iN^*}$	
			$N^* = \left(\frac{m+h}{i}\right)\left(\frac{\alpha-\beta}{\alpha}\right)$	

Notes: $\chi^1 = 1 + \frac{e}{n'} + \frac{e}{d} + \frac{\alpha e}{\beta m}$ $\chi^2 = 1 + \frac{e}{d+h} + \frac{\alpha de}{\beta(m+h)(d+h)} + \frac{(e+h)}{n'}$

$$\chi^3 = 1 + \frac{(e+h)}{n'} + \frac{\alpha i'(e+h)}{(\alpha-\beta)n'(m+h)} + \frac{n'e - \frac{\beta}{(\alpha-\beta)}i'(e+h)}{n'h}$$

if the nutrient cycle tends to be closed, primary producers tend also to disappear.

When decomposers have the competitive superiority for nutrient uptake, i.e., the condition described in Eq. 23 is not fulfilled, decomposers stay carbon limited. Then the decomposers' C-limited steady state is reached and the ecosystem persists, with coexistence of primary producers and decomposers.

Thus, the results obtained with the LVO model do not differ qualitatively from those of the LVC model, except that the external input of nutrient to the system allows the persistence of primary production even when decomposers disappear.

Concerning the DCO model, note that coexistence between primary producers and decomposers is possible for the two types of decomposer limitation (Table 2).

Considering the stability and feasibility conditions of the steady states, one can easily show that the following condition determine if decomposers will be C or N limited at steady state:

$$i' \left(\frac{\beta(d+h)(e+h)}{(\alpha-\beta)de} \right) < n' \quad (24)$$

i.e., when the decomposer immobilization rate i' is sufficiently small compared with the primary producer nutrition rate n' , the system reaches the N-limited decomposer steady state. On the other hand if this condition is not respected, the system reaches the C-limited decomposer steady state.

Thus, the results of the DCO model are qualitatively different from those of the DCC model in that ecosystem persistence no longer depends on the nature of decomposer limitation. The sink property of the detritus observed in the DCC model appears to be dependent on the strict closure of the system. The carbon limitation hypothesis does not hold in the DCO model, but when the dilution rate h tends to zero, the DCO model converges to the DCC model and the ecosystem tends to collapse when decomposers are nutrient limited.

DISCUSSION

Our model may be viewed as a minimal ecosystem model, which contains the most basic structural and functional aspects typical for ecosystems in general. The two key actors of ecosystems, primary producers and decomposers, are linked by an indirect mutualism mediated by material cycling, in which primary producers provide energy and nutrients to decomposers via detritus production, and decomposers renew nutrients for the primary producers through mineralization of the detritus nutrient stock. But stoichiometric constraints on carbon and nutrients also lead to an indirect resource competition between primary producers and decomposers for the nutrient limiting plant growth.

This dual, both mutualistic and competitive, indirect interaction between primary producers and decomposers makes ecosystem persistence a question in its own right. Our model shows that the primary producer-decomposer system is generally persistent (both living compartments reaching a stable positive steady state) only if decomposer growth is limited by the availability of carbon in the detritus, in agreement with the carbon limitation hypothesis (Currie and Kalff 1984). However, this is not a sufficient condition, and persistence also requires conditions depending on the difference between the carbon:nutrient ratios of primary producers and decomposers. The first condition is fulfilled when the competitive ability of decomposers for the limiting nutrient in inorganic form is sufficiently large compared with that of primary producers to maintain themselves in a state of carbon limitation. When decomposers are not competitive enough, they become nutrient limited, and the system eventually collapses. Our model further shows that the threshold competitive

ability of decomposers required to maintain them under carbon limitation hinges on the difference between the carbon:nutrient ratios of primary producers and decomposers: the larger this difference, the more competitive the decomposers have to be to keep the system persistent.

These conclusions hold when primary producers and decomposers tend to exert competing controls on the inorganic nutrient (recipient-controlled resource consumption of a Lotka-Volterra form in LVC and LVO models). In this case, the competitive exclusion principle applies, irrespective of whether the material cycle is closed or open. When the material cycle is open, however, the primary producers survive without the presence of decomposers because they are still supplied by the external input of nutrient into the system.

When there is no control of inorganic nutrient by primary producers and decomposers (donor-controlled resource consumption in DCC and DCO models), competitive exclusion should not occur, but our model shows that the above conclusions still hold if the material cycle is closed. When the material cycle is open, however, coexistence between primary producers and decomposers is possible even when they are both limited by the same nutrient. The cause of ecosystem collapse when the material cycle is closed is different from recipient-controlled models. In a closed donor-controlled model, the primary producer nutrition and decomposer immobilization fluxes are both controlled by the inorganic nutrient pool when decomposers are nutrient limited. As a result, the inorganic nutrient pool ultimately controls all the fluxes and stocks in the system, thus preventing any steady state from being reached. In contrast, when the material cycle is open, the inorganic nutrient pool is renewed in part by an external process, which stabilizes the system and allows its persistence even when primary producers and decomposers are both limited by the same nutrient.

The four applications considered in this paper do not include the allochthonous input of organic carbon that is presented in the general model. The absence of such input seems realistic for terrestrial ecosystems, but not for aquatic ecosystems, especially limnetic systems, which are known to sometimes support large inputs of organic matter (Hessen and Tranvik 1998). Such an allochthonous supply of organic matter would set the decomposers free from primary producers for their energy supply. Thus, by symmetry with the opening of the nutrient cycle considered in LVO and DCO models, which allow the persistence of primary producers when decomposers are excluded, it would allow the persistence of decomposers when primary producers are excluded from the system. This conclusion agrees with the results obtained experimentally in chemostat systems with allochthonous source of glucose (Pengerud et al. 1987). In this experiment, the authors showed that bacteria excluded algae when the loading of allochthonous organic carbon reached a threshold value,

and survived on glucose as the energy supply. The mechanistic determinism of this threshold value and its stoichiometry components, however, need further theoretical exploration.

A major conclusion that emerges from this study is that ecosystem persistence cannot be taken for granted. It is a nontrivial question, which depends on the fulfillment of strict conditions. How these conditions are met in real ecosystems becomes a new area of research.

Competitive ability and limitation status of decomposers

Experimental studies indicate that heterotrophic bacteria (which are responsible for the immobilization process) outcompete primary producers for nutrient uptake (Rhee 1972, Currie and Kalff 1984, Pengerud et al. 1987, Jackson et al. 1989). This result seems to be generally true in both terrestrial ecosystems where nitrogen is often the limiting factor, in freshwater ecosystems where phosphorus is often the limiting factor, and in marine ecosystems where nitrogen and/or phosphorus are limiting factors, even though this is still controversial. This is consistent with our model predictions, which show that, in a persistent system, bacteria should be competitively superior over primary producers. Other studies even indicate that decomposers have the ability to "take what they need" in terms of nutrients and stay carbon limited (Harte and Kinzig 1993, Kaye and Hart 1997). We show in this paper that such a situation does not contradict the control of inorganic nutrient by primary producers, which is also documented in the literature (Tilman 1982).

Our model assumes a strong competitive interaction between primary producers and decomposers for the same nutrient. Evidence of escape mechanisms, such as nutrient uptake in organic form by primary producers, or differences in the affinities of primary producers and bacteria for ammonium or nitrate has been established by several studies (Jackson et al. 1989, Kaye and Hart 1997). Thus, it seems critical that we learn more about the details of the competition between primary producers and decomposers.

In general, the literature is ambiguous with regard to what exactly limits decomposers. Some studies support carbon limitation (Bird and Kalff 1984, Vadstein et al. 1989, Kirchman and Richard 1990, Tuomi and Kuuppo 1999), whereas others conclude that decomposers are limited by the nutrient that limits primary production (Morris and William 1992, Thingstad et al. 1998, Zohary and Robarts 1998). Our theoretical results would tend to support carbon limitation in that they show that decomposers should be carbon limited to have a permanent ecosystem. However, we propose two explanations for the potential existence of ecosystems in which decomposers are nutrient limited instead of carbon limited.

First, nutrient limitation might be a transient situation in systems that are not at steady state. Once per-

turbed from its stable persistent steady state with carbon limitation of decomposers, an ecosystem can reach a situation of nutrient limitation for some time before returning to its stable steady state. In fact, most of the field studies that have observed nutrient limitation of decomposers have covered only one season, a time span that represents less than the total turnover of the system. These results may thus be transient seasonal phenomena.

Second, primary producers and/or decomposers might be controlled by a factor other than their resources. According to the extended competitive exclusion principle, two competitors can coexist on the same resource if one or both of them are controlled by another limiting factor, such as a predator (Levin 1970). Thingstad and collaborators (Thingstad and Pengerud 1985, Thingstad and Lignell 1997, Thingstad et al. 1998) have developed models showing coexistence of algae and bacteria when both are nutrient limited but controlled by predation (zooplankton and bacterivorous protozoa) in aquatic ecosystems. Other studies (Currie 1990, Tuomi and Kuuppo 1999) provide empirical evidence for such a scenario in a freshwater ecosystem. There is growing evidence for control, at least for short periods of time, of decomposers and/or primary producers by bacterivores and herbivores. In aquatic ecosystems, algae are often controlled by zooplankton, and bacteria responsible for nutrient immobilization are known to support important food webs (Azam et al. 1983, Naeem and Li 1998, Wickham 1998). In soils, bacteria are also known to support heterotrophic food webs where top-down controls are possible (Saetre 1998). However, our knowledge of control mechanisms in complex food webs is still incomplete. Thingstad et al.'s (1998) models hypothesize only one upper trophic level controlling algae and bacteria, which is an oversimplification of real food webs. Considering more trophic levels might change the picture completely because the control of a compartment depends on the number of upper trophic levels (Oksanen et al. 1981). Thus, making theoretical predictions on the control of bacteria and primary producers would require a good knowledge of the structure of in complex food webs and the predation functions, and this knowledge is still very limited for bacteria, particularly in soil detritus food webs (Zheng et al. 1997). One should not underestimate other potential regulating factors of bacterial growth, such as viral lysis (Amblard et al. 1998, Tuomi and Kuuppo 1999), physical factors such as temperature (Amblard et al. 1998), or water availability for terrestrial systems.

Our model does not take into account the links of the primary producer-decomposer system with the other functional groups of the ecosystem, such as herbivores and bacterivores. In this paper, we have intentionally reduced our approach to the primary producer-decomposer system because this is the basis of a minimum ecosystem in terms of function, in that it provides

primary production and nutrient recycling. It is important to understand the behavior and persistence conditions of such a system before considering upper trophic levels. It will then be important to assess whether or not upper trophic levels play a role in ecosystem persistence via the control of primary producers and decomposers, as already discussed, but also via the recycling processes. The literature is prolific concerning the recycling role of herbivores (Sterner 1990, Loreau 1995, Andersen 1997, de Mazancourt et al. 1998) and bacterivorous protists (Thingstad and Pengerud 1985).

Despite these controversies, the carbon limitation hypothesis seems to be consistent with some empirical data. In a recent paper, Jansson (1998) considered both the competitive ability and limitation status of bacteria, and argued that the dominance of mixotrophic microflagellates in phytoplankton communities of humic lakes could be explained by the carbon limitation hypothesis (Jansson 1998). Humic lakes are characterized by high inputs of allochthonous dissolved organic carbon. Bacteria are then relieved from carbon limitation, become phosphorus limited, and outcompete phytoplankton for phosphorus. The low concentrations of dissolved phosphorus lead to the dominance of mixotrophic phytoflagellates that retrieve phosphorus by ingestion of bacteria. Thus phytoplankton communities are dominated by mixotrophs that are limited by nitrogen rather than phosphorus, because the phosphorus:nitrogen ratio of bacteria they ingest is high. The system thus "escapes" the primary producer exclusion promoted by the external input of carbon, by reaching a situation where primary producers and decomposers are limited by different nutrients.

Experimental approaches of the competitive ability and limitation status of decomposers would be of high interest to test whether the carbon limitation hypothesis can be generalized to most ecosystems or whether upper trophic levels determine the limiting status and coexistence of primary producers and decomposers.

Sensitivity of ecosystem persistence to carbon : nutrient ratios

Our results suggest that the carbon : nutrient ratios of primary producers and decomposers play a critical role in ecosystem persistence. Coexistence at steady state of primary producers and decomposers is made easier by more similar ratios. Given this sensitivity of ecosystem persistence to the difference between the two ratios, factors that affect these ratios may play an important role.

According to recent studies, plant carbon : nutrient ratios change with the ratio between mineral nutrient and atmospheric CO₂, and an increase in atmospheric CO₂ concentration would lead to an increase in carbon : nutrient ratio of plant communities (Rastetter et al. 1997). On the other hand, the plasticity of the decomposer carbon : nutrient ratio is still controversial (Gold-

man et al. 1987, Vadstein et al. 1988). If the plant ratio increased and the decomposer ratio stayed constant, the difference between the two ratios would increase, thus potentially promoting ecosystem destabilization. Simulations with more detailed models, parameterized with realistic data, would be important to investigate whether global change in atmosphere CO₂ be able to contribute to such an ecosystem destabilization.

Another major factor determining the carbon : nutrient ratios of the plant or decomposer communities is interspecific competition within each community. If each species has its own ratio, the dominance of a particular species will have an impact on the mean ratio in the community. Thus both external physical factors, such as global change in atmospheric CO₂ concentration, and internal biological factors, such as interspecific competition, are able to affect the carbon : nutrient ratios of the primary producer and decomposer compartments and hence the conditions for ecosystem persistence.

Conclusion

Despite its simplicity, our model sheds new light on the question of the coexistence of primary producers and decomposers. It shows that, because of stoichiometric constraints, this question is far from trivial. Since this coexistence is the key to primary production, it is a *sine qua non* condition for ecosystem persistence. The main factors allowing this coexistence raise important questions for community ecology, ecosystem functioning, cell physiology, and global change. Experimental and empirical data concerning ecological stoichiometry are lacking (Tang and Dam 1999), and more research should be performed, including research on the external physical factors that influence the coupling of chemical elements in the biomass, or evolutionary trends (Elser and Urabe 1999). In light of our conclusions, it appears to us important that theoretical and experimental studies on primary producer-decomposer interactions be developed in various ecosystems. This would improve our knowledge of the major factors determining coexistence, such as the competitive ability of primary producers and decomposers for nutrient uptake, their limitation status, the factors that control their communities and the factors that determine their carbon : nutrient ratios. To this end, experiments in microcosms would be valuable, because they allow (1) the control of important functional processes represented in our model, such as the opening of the material cycle, the presence or absence of bacterivores and herbivores, and the control of factors limiting primary producers and decomposers; and (2) the identification of the transient and long-term dynamics of the studied ecosystems.

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APPENDIX A

An outline of the conditions of ecosystem persistence for the LVC model: local stability and feasibility analysis for the three steady states is available in ESA's Electronic Data Archive: *Ecological Archives* E082-032-A1.

APPENDIX B

An outline of the conditions of ecosystem persistence for the DCC model: local stability and feasibility analysis for the two steady states is available in ESA's Electronic Data Archive: *Ecological Archives* E082-032-A2.