



# Biotic regulation of non-limiting nutrient pools and coupling of biogeochemical cycles



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## ARTICLE INFO

### Article history:

Received 27 December 2015

Received in revised form 16 April 2016

Accepted 19 April 2016

### Keywords:

Anthropogenic impacts

Biogeochemical cycles

Nutrient cycling

Nutrient limitation

Regulation

Resource access limitation

## ABSTRACT

Anthropogenic activities heavily affect biogeochemical cycles at global scales; thus it is critical to understand the degree to which these cycles can be regulated by organisms. Autotrophs can regulate nutrient abundance through resource consumption, but their growth should not be affected by changes in the supply of non-limiting nutrients. Here we present a model where autotrophs consume two nutrients – one limiting and one non-limiting nutrient – and access only part of the nutrients available in the environment. We apply our model to the oceanic cycles of iron and phosphorus to examine whether phytoplankton can regulate the concentrations of these key nutrients and how interactions between the two cycles affect their regulation efficiency. Our model predicts that autotrophs cannot efficiently regulate concentrations of the non-limiting nutrient. We show that changes in the supply of the limiting nutrient affect the concentrations of the non-limiting nutrient, and that the two nutrients vary in opposite directions. Our results suggest that interactions between biogeochemical cycles can result either in an increase or in a decrease in the regulation efficiency of nutrient concentrations, depending on whether the supplies of the limiting and non-limiting nutrients vary in the same or opposite directions due to anthropogenic activities.

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## 1. Introduction

Biogeochemical cycles are heavily altered by anthropogenic activities at global scales due to climate change, rising atmospheric carbon dioxide and excess nutrient inputs (Denman et al., 2007; Canadell et al., 2010; Doney, 2010; Ciais et al., 2013). Supplies of key nutrients such as carbon, nitrogen, phosphorus and oxygen to terrestrial and marine biogeochemical cycles are heavily affected by agricultural activities, land-use change and burning of fossil fuels (Seitzinger et al., 2005; Gruber and Galloway, 2008; Bouwman et al., 2009). Given these massive alterations, it is critical to assess the extent to which biotic and abiotic processes can lead to regulation of biogeochemical cycles at global scales.

Biotic regulation of the Earth system is the subject of a long-standing debate, especially concerning the Gaia hypothesis, which assumes that organisms maintain environmental conditions in a habitable range through self-regulating feedback mechanisms (e.g. Lovelock and Margulis, 1974a,b; Margulis and Lovelock, 1974).

By modifying their environment through resource consumption, metabolism and habitat modification, organisms create strong feedbacks with their local environment (Kylafis and Loreau, 2008, 2011). However, these processes do not necessarily result in regulation of the global environment because resource access is generally limited in space due to physical or chemical barriers (e.g. Ruardij et al., 1997; Ostertag, 2001; Menge et al., 2008; Vitousek et al., 2010). For instance, in marine and other aquatic systems, physical resource access limitation is usually due to the presence of a pycnocline because of the warming of surface waters when solar radiation is high and vertical exchanges in the water column are low (Vallis, 2000). As photosynthetic activity depletes nutrients in the surface layer and the barrier of density limits water exchanges with deep waters (Falkowski and Oliver, 2007), most of the nutrients in the water column are inaccessible to phytoplankton.

Interactions between the geosphere, atmosphere and biosphere result in the coupling of biogeochemical cycles. For example, autotrophs, which use light to assimilate carbon dioxide and inorganic nutrients simultaneously, create a strong coupling between the biogeochemical cycles of key elements such as carbon, nitrogen and phosphorus as well as between these cycles and the global climate (Falkowski et al., 2000; Gruber and Galloway, 2008). Fossil-fuel combustion and food production release nitrous oxides and ammonia in the environment, which are deposited on the ground or in the water, thereby increasing the growth of plants

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**Table 1**  
Parameters of the stoichiometric model.

Symbol	Description	Units
$\alpha$	Fraction of the system that is accessible to organisms	
$m$	Mortality rate of autotrophic organisms (including grazing)	$\text{yr}^{-1}$
$\mu$	Maximum growth rate of autotrophic organisms	$\text{yr}^{-1}$
$R$	$\text{N}_2:\text{N}_1$ ratio of autotrophs	
$N_{H,n}$	Half saturation constant of the growth of autotrophic organisms for the nutrient $n$ in accessible form	$\mu\text{mol m}^{-3}$
$\lambda_n$	Fraction of organic matter that is not recycled in nutrient $n$	
$rec_{a,n}$	Fraction of recycling of nutrient $n$ that occurs in the accessible pool	
$k_{a,n}$	Transfer rate of nutrient $n$ from the accessible to the inaccessible pool	$\text{yr}^{-1}$
$k_{i,n}$	Transfer rate of nutrient $n$ from the inaccessible to the accessible pool	$\text{yr}^{-1}$
$S_{a,n}$	Supply of nutrient $n$ to the accessible pool	$\mu\text{mol m}^{-3} \text{yr}^{-1}$
$S_{i,n}$	Supply of nutrient $n$ to the inaccessible pool	$\mu\text{mol m}^{-3} \text{yr}^{-1}$
$q_{a,n}$	Turnover rate of nutrient $n$ in the accessible pool	$\text{yr}^{-1}$
$q_{i,n}$	Turnover rate of nutrient $n$ in the inaccessible pool	$\text{yr}^{-1}$

or phytoplankton and their uptake of atmospheric carbon dioxide (Gruber and Galloway, 2008).

Redfield ratios in the ocean provide one potential example of biotic regulation of the global environment that implies interactions between nutrient cycles (Auguères and Loreau, 2015a). Analysis of the composition of phytoplankton cells shows a mean N:P ratio of 16N:1P (Redfield, 1934; Fleming, 1940), similar to the N:P ratio of 15N:1P in deep waters obtained through the analysis of seawater samples (Redfield, 1934, 1958). The N:P ratio of deep waters can differ from the Redfield ratio due to changes in the N:P ratio of the material that is supplied to the ocean and in microbial activity, e.g. anammox (i.e. microbial process of anaerobic ammonium oxidation which releases  $\text{N}_2$ ), denitrification and nitrogen fixation (Gruber and Sarmiento, 1997; Karl, 1999; Karl et al., 2001; Arrigo, 2005). The diversity of phytoplankton communities and their spatial distribution can also create regional deviations from the Redfield ratio in deep waters (Weber and Deutsch, 2010; Weber and Deutsch, 2012). However, the deep-water N:P ratio seems to be almost constant over space and time, which suggests that biotic processes such as nitrogen fixation and denitrification control the proportions of N and P in seawater (Redfield, 1958; Tyrrell, 1999; Lenton and Klausmeier, 2007; Weber and Deutsch, 2010; Weber and Deutsch, 2012; Auguères and Loreau, 2015a).

Previous theoretical studies on biotic regulation of biogeochemical cycles have focused on regulation of the concentration of a single limiting nutrient (Auguères and Loreau, 2015b), or of the concentrations of two nutrients that limit the growth of two functional groups of organisms (e.g. Tyrrell, 1999; Lenton and Watson, 2000; Auguères and Loreau, 2015b). The ability of autotrophs to regulate nutrient concentrations in their environment, however, should be different for limiting and non-limiting nutrients. Interactions between nutrient cycles can also alter the concentration of nutrients in the environment, and thus their regulation by organisms. Our goal in this work is thus to elucidate the ability of autotrophs to regulate the pools of non-limiting nutrients in both accessible and inaccessible form at large spatial and temporal scales, as well as the interactions between the cycles of a limiting nutrient and a non-limiting one. We first develop and analyse a stoichiometric model of resource regulation with resource access limitation. Contrary to models applied to Redfield ratios in the ocean (e.g. Tyrrell, 1999; Lenton and Watson, 2000; Auguères and Loreau, 2015b), our model describes the dynamics of a single population of autotrophs. Both inorganic nutrients – one of which is limiting and the other is non-limiting for the growth of autotrophs – occur in two pools, one accessible and the other inaccessible to autotrophs. We then apply our model to the specific case of the regulation of iron (Fe) and phosphorus (P) in the global ocean. We parameterise our model of coupled P and Fe cycles with existing data, and analyse the potential for biotic regulation of Fe and P concentrations as well as their ratio with respect to changes in the supply of both Fe and P. This case

study is of special interest since Fe and P often limit phytoplankton growth (Moore et al., 2001; Moore and Doney, 2007; Moutin et al., 2008; Monteiro et al., 2011), and their supply to the surface ocean is heavily impacted by human activities (Benitez-Nelson, 2000; Mahowald et al., 2005; Krishnamurthy et al., 2010).

## 2. Materials and methods

We extend a previous model of resource regulation with resource access limitation (Auguères and Loreau, 2015b) to the biogeochemical cycles of two nutrients. In this model, nutrients occur in two pools, one that is accessible to autotrophs, and the other that is inaccessible to them, because of either physical or chemical barriers.  $N_{a,1}$  and  $N_{a,2}$  are the concentrations of nutrients 1 and 2, respectively, in the accessible pool.  $N_{i,1}$  and  $N_{i,2}$  are their concentrations in the inaccessible pool. Autotrophs, whose concentration in the accessible pool is  $B$ , consume nutrients in that pool. To differentiate the characteristics of the two nutrient cycles, we add a subscript corresponding to the nutrient considered (i.e. 1 or 2) to all the variables and parameters described in Auguères and Loreau (2015b). Model parameters are described in Table 1. The only parameter that is specific to the present stoichiometric extension of the model is the stoichiometric ratio of autotrophs ( $R$ ), i.e. the ratio of nutrient 2 to nutrient 1 in autotrophs. For the sake of simplicity, this stoichiometric ratio is supposed to be constant. The fraction  $\alpha$  of the total volume of the system (i.e. the sum of the volumes of both accessible and inaccessible pools, noted  $V_a + V_i$ ) that is accessible to organisms is supposed to be the same for both nutrients. This assumption, which we make for the sake of simplicity, should hold in the case of physical limitation, where physical barriers usually constrain the accessibility of all the nutrients in the same way. In the case of chemical limitation, the accessible and inaccessible forms of each nutrient occur in the same volume (i.e.  $V_a = V_i$ ), and thus  $\alpha = V_a/(V_a + V_i) = 0.5$  for both nutrients.

The principle of mass balance is used to build a model that describes nutrient masses in each pool. By dividing nutrient mass by the volume of the pool concerned, we then obtain a model in terms of nutrient concentrations (Fig. 1):

$$\begin{aligned}
 \frac{dN_{a,1}}{dt} &= S_{a,1} - (k_{a,1} + q_{a,1})N_{a,1} + \frac{1-\alpha}{\alpha}k_{i,1}N_{i,1} + (mrec_1(1-\lambda_1) - G)B \\
 \frac{dN_{a,2}}{dt} &= S_{a,2} - (k_{a,2} + q_{a,2})N_{a,2} + \frac{1-\alpha}{\alpha}k_{i,2}N_{i,2} + (mrec_2(1-\lambda_2) - G)RB \\
 \frac{dN_{i,1}}{dt} &= S_{i,1} + \frac{\alpha}{1-\alpha}k_{a,1}N_{a,1} - (k_{i,1} + q_{i,1})N_{i,1} + \frac{\alpha}{1-\alpha}m(1-rec_1)(1-\lambda_1)B \\
 \frac{dN_{i,2}}{dt} &= S_{i,2} + \frac{\alpha}{1-\alpha}k_{a,2}N_{a,2} - (k_{i,2} + q_{i,2})N_{i,2} + \frac{\alpha}{1-\alpha}m(1-rec_2)(1-\lambda_2)RB \\
 \frac{dB}{dt} &= (G - m)B
 \end{aligned}
 \tag{1}$$

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