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LETTER

The human-induced imbalance between C, N and P in Earth's life system

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Abstract

Human-induced carbon and nitrogen fertilization are generating a strong imbalance with P. This imbalance confers an increasingly important role to P availability and N : P ratio in the Earth's life system, affecting carbon sequestration potential and the structure, function and evolution of the Earth's ecosystems.

Keywords: CO_2 fertilization, eutrophication, evolutive driver, N and P deposition, N : P ratio

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Is global C and N fertilization leading to enhanced P limitation?

Humans are continuously raising atmospheric CO_2 concentrations by increasing fossil fuel combustion (IPCC, 2007). In addition to a warming effect, the increasing atmospheric CO_2 concentrations can have a stimulating effect on plant primary productivity, thus increasing the ecosystems' capacity of storing more carbon and mitigating the rise of atmospheric CO_2 concentrations (IPCC, 2007; Data S3).

However, this fertilizing effect is strongly dependent on nutrient availability (Reich *et al*., 2006). With increasing growth, more nutrients become immobilized in biomass and soil organic matter. Thus, increased nutrient availability needs to accompany higher plant photosynthetic rates (Reich *et al*., 2006). Without a higher availability, nutrients, especially N, the main macronutrient, could become a limiting factor in plant primary productivity's capacity to buffer human-induced increases in atmospheric CO_2 concentrations (Reich *et al*., 2006).

Notably, this possible N limitation may be overcome by the continuously increasing release of reactive N into the biosphere from fossil fuel burning, crop fertilization and anthropogenic N_2 fixation (legume and rice crops). These anthropogenic N inputs into the biosphere amount to roughly 165–259 Mton N $year^{-1}$, that is, close to the total amount of N fixed naturally in the continents and the oceans altogether (Fig. 1). As a result, atmospheric reactive N deposition has increased globally from 32 Mton N $year^{-1}$ in 1860 to ~112–116 Mton N $year^{-1}$ nowadays (Fig. 2). Current projections expect a further enhancement that will raise the total global annual N deposition to approximately twofold the current levels by 2050 (Fig. 1). These enhanced N inputs have already been shown to affect ecosystem structure and function (Janssens *et al*., 2010). Among these effects, a net sink for N on land is consistent with an apparent increasing carbon sink in terrestrial biomass from the 1990s to present, mainly in temperate areas of Eurasia and North America, where several forests are growing on former agricultural land which was abandoned a few decades ago (Data S3).

However, there are several studies that report no significant increases or even reductions in global tree growth and global carbon sinks, despite the increase in atmospheric CO_2 concentrations, and despite the general increase in N deposition (Peñuelas *et al*., 2011). These results suggest that other factors have overridden the potential growth benefits of a CO_2-rich world at many sites. It is thus still uncertain how this N increase affects the global C cycle. This uncertainty is linked, among other factors such as water availability, to the possible limiting role of other nutrients and their interactions (Reich *et al*., 2006).

Among these other nutrients that are expected to become limiting to net primary productivity, P appears to be crucial. P is present in the structure of DNA, in cell membranes, in many enzymes, in molecules storing and supplying energy and in bones. Despite its ubiquitous relevance, it is relatively scarce in the envi-

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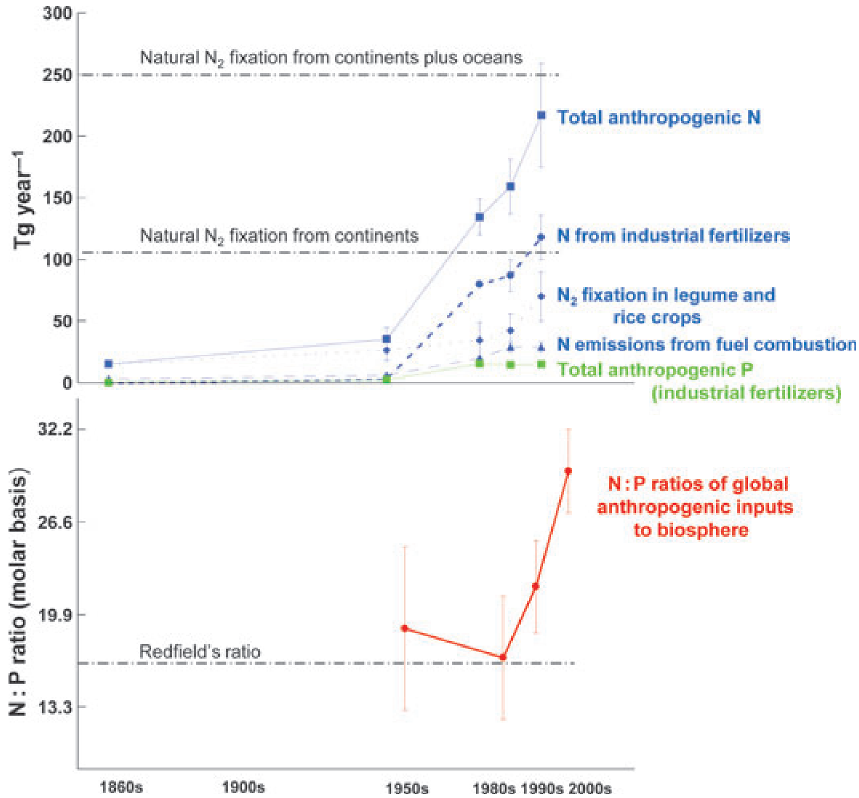

Fig. 1 (a) Anthropogenic reactive N and P inputs to the biosphere (Tg year^{-1}) since the industrial revolution (1860), and (b) the N : P ratio (on mass and molar basis) of the reactive N and P anthropogenic inputs to the biosphere. Bars represent the range of the data reported (details and references in Table S1).

ronment and could become more limiting if C and N inputs continue to increase substantially. In fact, coinciding with N deposition, some studies have already observed an increase in the N : P ratio of terrestrial and aquatic organisms (Elser *et al.*, 2009; Data S3). There are even some observations in certain ecosystems showing that an increased N deposition has led to a shift from N to P limitation (Vitousek *et al.*, 2010).

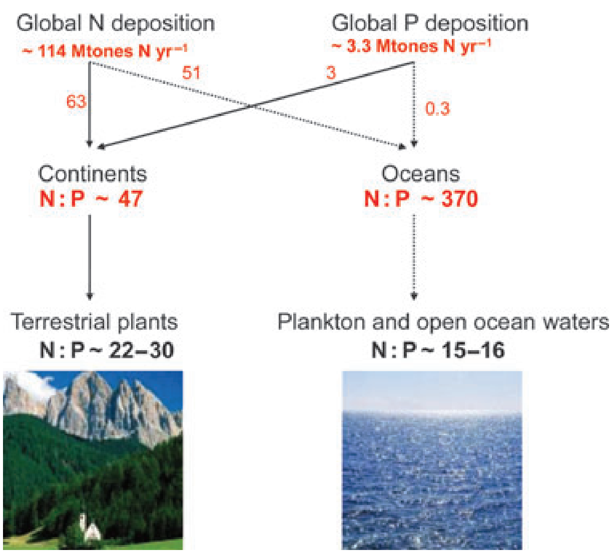

Fig. 2 N : P ratios (on a molar basis) of global atmospheric deposition in continents and oceans, compared with those of plants and waters (details and references in Table S2).

P limitation could thus play a far underestimated role in ecosystems' C-storing capacity (Peng & Thomas, 2010). P can have a direct influence on C-storing capacity of terrestrial and aquatic ecosystems through its effect on plant growth capacity (Data S3). P can also have an indirect effect on C-storing capacity through its determining role in N_2 fixation, because insufficient availability of P and other nutrients such as K, Si or Mo limits the activity of free living and symbiotic N_2 fixing organisms in both terrestrial and aquatic ecosystems (Data S3).

Human activity tends to fertilize the biosphere with P, but at a smaller rate than the increases in the availabilities of C and N resulting in increasingly higher biospheric N : P ratios (Fig. 1). There are two main reasons why P fertilization is less than C and N fertilization. First, C and N fertilization originate mainly from sources that do not seem to have an immediate limit (fossil fuels, industrial fertilizers obtained from the Haber–Bosch reaction between atmospheric nitrogen and hydrogen at elevated pressure, anthropogenic N_2 fixation), while P fertilization comes mainly from rocks and sediments with limited occurrence. Second, while C and N are highly mobile and globally widespread, P compounds are much less mobile and typically confined to specific areas. These differences confer on P a particularly limiting role in ecosystem C storage and in the ecological and evolutive traits of species and ecosystems.

Eutrophication: global N : P increase vs. local agricultural N : P decrease

In spite of its great variability, the N : P ratio on a molar basis tends to reach on average 14–16 in ocean plankton and 22–30 in terrestrial and freshwater plants (Figs 1 and 2). Fossil fuels, fertilizers and anthropogenic N_2 fixation products, all have much higher N : P ratios.

Fossil fuels are disproportionately richer in N (1000–20 000 mg L^{-1}) than in P (at the level of a few mg L^{-1}; Data S3). Thus, the C : N, C : P and N : P ratios in fossil fuels are much higher than in plants, both in ocean and in terrestrial ecosystems (Data S3). Furthermore, whereas annual emissions of N from fossil fuel combustion reached 33 Mton in 2000, there is no global evidence of a significant global flux of P to the atmosphere.

Regarding fertilizer application, the availability of N of anthropogenic origin has grown fourfold since the 1960s, and continues to increase (Table S1). There has also been approximately a fourfold increase in P inputs to the biosphere in the period from the 1950s to 1980s primarily because of the mining of P compounds for fertilizers, But the inputs have remained more or less constant since 1989 (Fig. 1), thus further contributing to disproportionately higher N : P ratio inputs in most ecosystems. The global use of P fertilizers by farmers is ~17 Mton of mined P whereas the global N inputs from fertilizers are considerably higher, 100–136 Mton N $year^{-1}$ (Fig. 1). To these amounts of N and P provided by fertilizers we must add the anthropogenic N_2 fixation (legumes and rice crops) that is currently estimated at ~40–90 Mton $year^{-1}$ of N depending on the study (Fig. 1).

In addition to these direct human inputs of fertilizers, there is also atmospheric N deposition of ~48–54 Mton N $year^{-1}$ in oceans and of ~63 Mton N $year^{-1}$ in terrestrial ecosystems (Fig. 2). Global P deposition represents 3–3.5 Mton $year^{-1}$, mostly coming from wind-eroded particles and biomass burning aerosols. Of this global P deposition ~90% occurs in continents and only ~10% in oceans. These data show a N : P deposition ratio (on a molar basis) of ~370 in the ocean, that is, more than 20 times the Redfield ratio of plankton and open ocean waters and ~47 in the continents, that is, twice the mean N : P ratios for most terrestrial plants (Fig. 2).

The total world N stored in terrestrial land plants is estimated as ~3500 Mton (Table S2). The N deposition inputs in terrestrial ecosystems in 1 year (~63 Mton) represent therefore nearly 2% of the total N contained in terrestrial plant biomass. The total N deposited in oceans (~51 Mton $year^{-1}$) is similar to the global river N inputs to oceans, but whereas the river N inputs have their greatest importance in coastal areas, the N deposited from the atmosphere is most important in open oceans, where it can be critical due to the low nutrient concentrations in general. In fact, in open ocean there is experimental evidence showing an expansion of P-limited areas in response to several global change drivers, but also in response to the increased N : P ratios of the atmospheric inputs (Fig. 2). Furthermore, in oceans, warming reinforces water column stratification and N_2 fixation capacity (Data S3), with a subsequent shift from N to P limitation in surface waters.

Globally, the integrated anthropogenic inputs to the biosphere have a N : P ratio of ~22.8–44.6 : 1 on a molar basis (Fig. 1). This ratio is nearly twice the average N : P contents ratio of plankton and on average 5–100% greater than the observed optimum soil N : P ratios (~16–22) for the growth of most terrestrial plants. All together suggests a global scenario of increasing P limitation, predominantly in marine ecosystems and also in terrestrial nonagricultural ecosystems.

However, in contrast to the global tendency to an enhancement of the N : P ratio, P is polluting some agricultural areas where it decreases the N : P ratio of waters in soil, lakes and streams. This occurs particularly in areas with intense pasture and animal slurry use for land fertilization (Data S3). In contrast, in areas dominated by crops fertilized solely with industrial fertilizers, streams and lakes have systematically shown high N : P ratios (Data S3). In any case, while N is more mobile and consequently tends to leach easily from crop soils to waters, P inputs from fertilizers tend to remain and accumulate in crop soils (Data S3).

Nonetheless, P may end up becoming limiting even in agricultural lands. The main source for P fertilizers is mined phosphate rock, whose demand is continuously increasing, and there is an emerging concern about the sustainability of such an increase. The problem may further be worsened by the fact that only five countries hold 90% of the world P reserves, making several world regions such as Europe, India and Indonesia completely dependent on P imports (FAO, 2008). In fact, in many developing countries, fertilizer applications are imbalanced, that is, too little P and K in relation to N, and this tendency is even apparent in developed countries (FAO, 2008).

All these inputs drive towards a scenario of a decrease in N : P in some cropland areas with high livestock densities, but with a much more general increase in the N : P ratio in other ecosystems (forest, oceans, lakes, some croplands). This latter tendency is likely to be exacerbated with further acceleration of the C and N cycles and with exhaustion of the P reserves.

Ecological and evolutive consequences of the altered N : P ratios

Shifts in the N : P ratio of the environment do not only affect the ecosystem's C storage capacity, but they can also have significant impacts on other ecosystem structural and functional traits. Increases in the N : P supply ratios of food sources may decrease the growth rates of consumers in different taxonomical groups such as unicellular organisms, zooplankton, fish and terrestrial plants and animals, although there are also exceptions (Peñuelas & Sardans, 2009). Only reduced allocation to ribosomal RNA is possible under P limitation, thus hindering high growth rates and favouring species with lower growth rates.

The changes in both the environment's and organisms' N : P contents ratio can have further long-term effects on organisms' and ecosystems' structure and function by determining even a DNA composition shift. Acquisti *et al*. (2009) compared the composition of the completely sequenced genomes of *Oryza sativa* and *Arabidopsis thaliana*, and used data from the TIGR database and available protein sequences of many domesticated and undomesticated plants. They found higher N content in genomes and proteomes in domesticated plants growing in N-rich soils than in undomesticated plants, growing in N-poor soils. Thus, under high N availability, selection would favour the use of N-rich nucleotides in plant genomes. These results suggest a possible role of N availability in the evolution of plant genomes and link genome evolution with the chemical composition of the environments within which biota evolve. This genomic effect could also occur with P availability, and in this way the N : P ratio could become an evolutive driver that affects from species genomes to ecosystem structure at medium as well as at longer time scales. Thus, the human-induced modification of N : P ratio of several ecosystems at world scale might be acting as an evolutive driver.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Anthropogenic reactive N and P inputs to the biosphere (Tg $year^{-1}$) and their N : P ratio (on mass and molar basis).
Table S2. N and P global atmospheric deposition in continents and oceans.
Data S3. Supplementary references.