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Land and ocean nutrient and carbon cycle interactions

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The biosphere's uptake and storage of carbon have the potential to either slow or amplify global warming providing a carbon-climate feedback to global warming. The interactions between carbon (C) and the nutrient cycles, especially nitrogen (N) and phosphorus (P), are important to the biosphere's storage of carbon. The century-scale carbon-climate feedback of the land is projected to be an order of magnitude greater than the ocean; however, the land's importance may have been overestimated as they are based on models that neglect nutrient limitation. The omission of N limitation reduces the negative carbon-climate feedback by up to 30%, and further, we postulate as N-deposition and N-fixation increase, P limitation will become important in limiting the future land carbon-climate feedback. Process-based C, N and P land models are needed to realistically project this century carbon-climate feedback. In the ocean, the carbon and nutrient cycles are tightly coupled as a result of low living biomass relative to its annual turnover. With rapid recycling of carbon and nutrients, the ocean carbon-climate feedback is weak at the century time-scale. The land and ocean C, N and P cycle models (earth system models) are needed for both improvement of projections of climate change and more realistic investigation of the impact of climate change on land and ocean ecosystems. An earth system modelling approach can also help to assess the impact of different processes on carbon and nutrient cycling, and identify where improved process-understanding is needed.

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Introduction

The CO_2 concentration in the atmosphere is an important driver of the earth's climate. The land and ocean play an important role in regulating atmospheric CO_2 and in the process provide a carbon-climate feedback to climate change. Since 1900, the land and ocean together have taken up about 60% of the anthropogenic carbon emissions [1] thus providing an important negative climate feedback to anthropogenic CO_2 emissions. The future role of this carbon-climate feedback is essential to projecting climate change. Modelling studies show that future warming will reduce the carbon uptake by land and ocean, resulting in more warming than predicted by models without a carbon cycle [2•]. Estimates of the responses by land and ocean to future climate and higher atmospheric CO_2 levels by present global models remain highly uncertain, between −6 Pg C/y and 11 Pg C/y for the land biosphere, and from 4 Pg C/y to 9 Pg C/y for the ocean by 2100 [2•].

How model projections handle the interactions between carbon, nutrient cycles and climate is an important issue. Recent studies have shown that nutrient limitation may impose a significant limitation on carbon uptake by the land biosphere leading to even greater warming than when nutrients are not limiting [3,4•,5••]. This paper explores the links between carbon (C), phosphorus (P) and nitrogen (N) cycles (henceforth referred as the nutrient cycle) and the potential for the land and ocean biospheres to provide a carbon feedback to climate change.

Carbon and nutrient cycling both on the land and in the oceans are intimately linked and both have an important influence on the carbon-climate feedback of the land [5••,6] and ocean biospheres (e.g. [7]). In the following sections, we review what we know about the interactions between carbon and nutrients cycles on land and in the ocean, and use this information to assess the potential carbon-climate feedback of the two biospheres on this century's climate.

Land biosphere

The cycling of carbon on the land is intimately linked to the cycles of N and P [8•]. As a result, net primary productivity (NPP) of most land ecosystems is either N or P limited [9]. The N and P cycles have generally been neglected in quantifying the carbon-climate feedback [1]. As highlighted in a recent study [5••], the projected increase n carbon stored on the land over the next century is reduced by up to 150 Pg C (30%) by the end of the century, when N limitation is included.

On the land, there are significant variations in the C:N:P ratios of organic matter globally across biomes [8•]; and across the various organic pools within each biome (e.g. plant biomass, litter and soil organic matter) [10]. The

land therefore has the capacity to increase carbon storage without a corresponding increase in nutrient uptake. The preferential pooling of the carbon in high C:N and C:P pools such as woody biomass and litter can increase the land carbon storage without increasing N and P demand. However, the current carbon models project over this century most of their increase in carbon storage in plant biomass rather than in litter pools suggesting this is not a dominant effect [5••]. This is due to the rapid turnover of litter pools [11]. Further, increased carbon storage in the plant biomass or soil carbon pools is not sustainable indefinitely without an increase in the availability of N and P at the ecosystem scale [12•]. To sustain model projected increase in land C storage out to 2100, an additional supply of nutrients to plants will be required through increases in net mineralization in the soil or external supply, or both.

On the land, the atmosphere supplies all the carbon to plants via photosynthesis, whilst the soil provides most nutrients required by plants, additional nutrient supplies include deposition for both N and P, biological N-fixation (converting N_2 in the atmosphere into NH_3) for N and weathering for P (Figure 1). Soil mineralization of N and P, and the biological N-fixation are both affected by environmental conditions (e.g. CO_2, temperature and rainfall) [13•]. Therefore the impact of nutrient limitation will evolve in the future and affect the sensitivity of the carbon pools in the land biosphere to atmospheric CO_2 levels and to climate [6].

Increased mineralization of soil N and P could supply more N and P, but it would be associated with increased C mineralization. Unless the extra N and P result in much greater C storage than the extra mineralized C, it will not substantially increase C storage on decadal to century time-scale. Indeed a simulation study [3] demonstrated that the predicted warming in high latitude regions by 2100 will increase the soil N mineralization and produce a small increase in total C storage.

The most efficient way to increase N availability is through biological N-fixation. For unmanaged land systems, biological N-fixation supplies 70% of the external N [5••,14•], and at present N-fixation accounts for 10 to 20% of the N required for global NPP (Figure 1) [5••]. In addition to being an important source of N, biological N-fixation is influenced by a myriad of environmental controls (e.g. light, C, nutrients and climate) [15••]. Although biological N-fixation is an important source of N and strongly influenced by climate change, it still remains poorly represented in land carbon models — it is either ignored or represented by correlation models, that is N-fixation set by correlations with model variables [4•,16] or based on simple process models [15••]. These approaches simulate large differences in the present rate of N-fixation and its response to climate change. For example, correlation models [4•] predict increased N-fixation with temperature [16] allowing the highest N-fixation in evergreen tropical rainforests. In contrast, the process-based models only predict increased N-fixation with increased temperature in the temperate and boreal region and decreased N-fixation with increased temperature in the tropics [15••], thereby allowing the highest N-fixation in tropical savannahs. The latter simulation is more consistent with field observations [5••]. The present uncertainty in simulated N-fixation rates and the response of N-fixation to climate change needs to be addressed, if one is to properly handle potential N-limitation and reduce the uncertainty of the estimated carbon-climate feedback of the land biosphere.

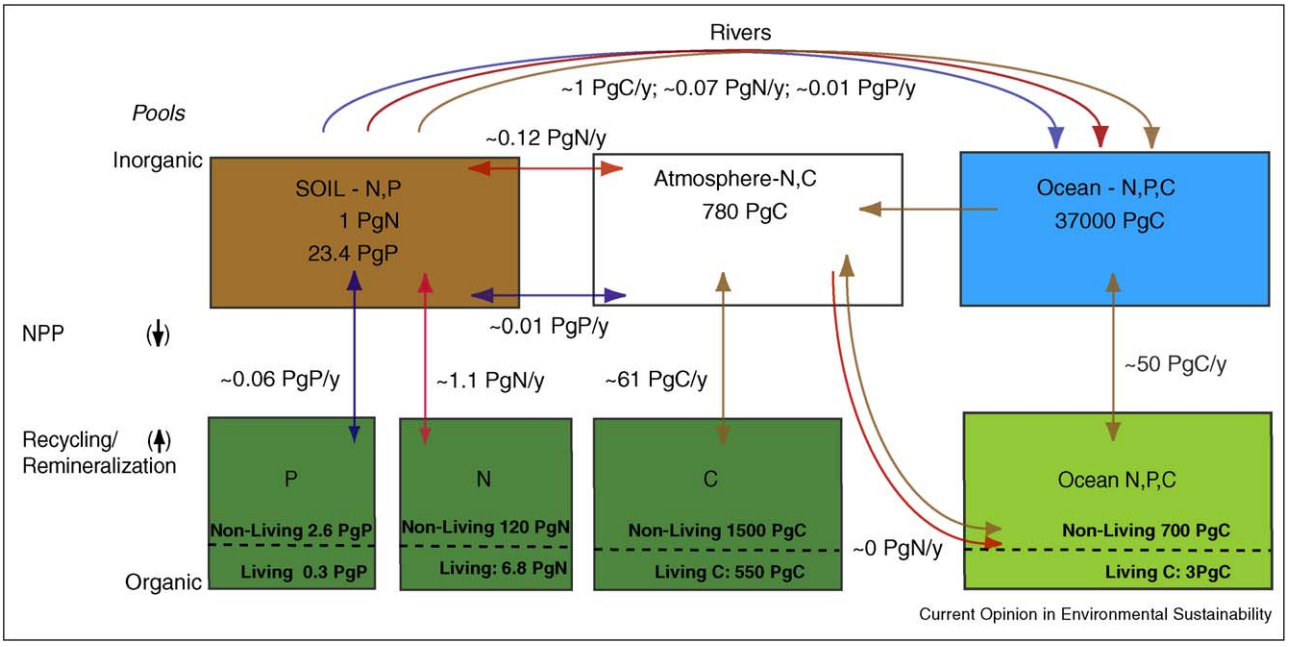
P limitation can also have significant negative effect on future land carbon storage. At present, NPP of most tropical forests and savannahs, which contributes to about 50% of global NPP of the land biosphere, is P limited. Present evidence suggests that the response of NPP to elevated atmospheric CO_2 levels is much smaller under P-limitation than under N-limitation [17]. The elevated atmospheric CO_2 and increased N-deposition can accentuate P limitation [18]. Further, at present, about 11% of the world's ecosystems receives sufficient anthropogenic N-deposition to meet their N requirements for NPP, by 2050 this is expected to double [19]. Importantly, with increased N-deposition we expect shifts from N to P limitation to occur in subtropical regions of the northern hemisphere [20]. Further, increased N-deposition will acidify the soil and reduce the P availability in the soil thereby accentuating P limitation.

To better project the potential carbon-climate feedback of the land biosphere requires land models that explicitly include the N and P cycles and an evolving climate. The inclusion of the N and P cycles and their interaction with the C cycle should be process-based exploiting our current understanding. In particular the modelling approach needs to include potential interactions between the C, N and P cycles such as: How N-fixation responds to climate change and elevated CO_2, and will this process alter the P availability? How P availability responds to climate change, increased atmospheric CO_2 and increased N-deposition? We may still lack adequate understanding to address all the potential C–N–P interactions but our existing knowledge is sufficient to provide assessments of how the N and P cycles alter the land's carbon-climate feedback over this century.

Ocean biosphere

Physical and biological processes together drive the exchange of carbon between ocean and atmosphere, and these exchanges may respond to climate change and rising atmospheric CO_2 levels, for example [7]. The physical carbon exchange is controlled by the ocean circulation, the level of atmospheric CO_2 and the amount

Figure 1



Schematic representation of the carbon (C), nitrogen (N) and phosphorus (P) pools and their interactions between organic and inorganic pools. The inorganic pools comprise the soil (brown box), the atmosphere (clear box) and the ocean (blue box). The organic pools for the land (dark green) and ocean (light green) are composed of both living and non-living organic matters. The approximate size of each of the pools is given for each box. Note for the soil, the inorganic pool P is large but only a few percent is biologically available. The transfer of C, N and P shown as black, blue and red arrows, respectively, between the atmosphere, inorganic and organic pools in the land and ocean are shown along with the approximate flows. The two-way arrows represent, potential feedbacks between different pools. The nitrogen exchange between the atmosphere and ocean represents exchanges due to nitrogen fixation and denitrification. Values of nutrient (P, N) and carbon transfer, inorganic and organic pools, are from [34••,35], respectively.

of warming in the surface ocean. Although the physical driven carbon exchange is important as it is the primary mechanism for the oceanic uptake of anthropogenic carbon, it can be considered independently of the nutrient cycle. Here we focus on the biologically driven ocean exchange of carbon with the atmosphere. This exchange involves the biological uptake of nutrients and carbon in the euphotic zone of the upper ocean, its subsequent biological remineralization back into its inorganic nutrients and carbon in the ocean interior and the physical resupply of the carbon and nutrients back into the euphotic zone. The inclusion of the ocean circulation in the carbon and nutrient cycles provides a delay to the impact of biological changes in the nutrient cycle and their impact on the carbon uptake.

In the upper ocean, biological processes transform inorganic carbon and nutrients into both particulate and dissolved organic matter (POM and DOM). The biological production and remineralization of particulate organic matter back into its inorganic form occurs at nearly fixed C:N:P [21]. This accounts for more than 80% of the organic matter generated in the euphotic zone. The POM is rapidly remineralized on a time-scale less than a year. The remaining 20% of biologically produced organic matter occurs as dissolved organic matter (DOM) with a higher and more variable C:N:P ratio, with a significantly longer lifetime (decades to multi-millennial) [22,23]. It is natural to consider whether changes in the C:N:P ratios in both of the POM and DOM pools may provide a mechanism for biological processes to change the amount of carbon sequestered by the ocean and thereby modify the rate of climate change.

Several mechanisms have been presented for how elevated CO_2 levels and climate change may alter the C:N:P of biological uptake. These include: first, elevated CO_2 levels in the ocean increasing the carbon content per unit of N and P of POM and increasing uptake (e.g. [24••,25]); second, increased CO_2 enhancing N-fixation, thereby relaxing N limitation and increasing CO_2 uptake [20]; third, changed physical environment, for example, increased light levels in response to increased stratification and ocean warming that favours phytoplankton species which are less efficient at exporting POM from the euphotic zone [26], and more efficient breakdown of DOM [22], both reducing CO_2 uptake; fourth, elevated CO_2 in the ocean increasing DOM production and the amount of C in the long lifetime DOM carbon pool and

increasing the carbon uptake [22]; fifth, ocean acidification may shift the ecosystem structure towards system that is less efficient at POM export from the euphotic zone and decreasing uptake [27].

As POM is exported from the euphotic zone and as DOM is transported by the ocean circulation they are remineralized by bacteria back into their inorganic constituents. Several mechanisms have been suggested for changing the C:N:P of the remineralized material: first, the ocean could preferentially recycle P:N:C of the POM and DOM (e.g. [28•,22], respectively); second, the projected expansion of the anoxic regions of the ocean through global warming and increased carbon export [28•,29••] could increase denitrification and lead to a loss of available N for phytoplankton growth; third, changing the depth of remineralization of the exported POM [30] and rate of DOM remineralization by changing the ocean's temperature and changing the type of material exported from the euphotic zone (e.g. changes in size, composition and aggregation).

An important feature of the ocean biosphere is the amount of carbon and nutrients in living biomass (3 Pg C) is much smaller than the land biosphere (Figure 1) but the total Net Primary Production (NPP) is of similar magnitude to the land biosphere (50 Pg C/y and 61 Pg C/y, respectively). Hence, the recycling (uptake and remineralization) of nutrients and carbon between the organic and inorganic pools in the oceans is in general much faster than on the land but it requires the ocean circulation to supply the nutrients and carbon back to the euphotic zone. To biologically increase the amount of carbon stored in the ocean there must be either an increase in the export of organic carbon into the ocean interior out of contact with the atmosphere or an increase in the carbon stored in long-lived DOM pool. On millennium time-scale changes in the remineralization of sinking organic carbon has an important influence on atmospheric CO_2[31]. However, when considering the potential carbon feedback over this century, because the exported organic matter is resupplied back into the euphotic zone on decadal time-scales, model simulations are therefore unable to produce more than 50 Pg C of increased uptake [28•,29••–30,32,33]. The resupply appears insensitive to whether one increases the C:N of the exported organic matter [28•,29••], deepens the remineralization of organic carbon [30], or tries to increase the supply of nutrient rich water to the surface regions that are nutrient limited [32,33]. It is this rapid resupply of the exported carbon and nutrients back into the surface ocean that accounts for the weak carbon-climate feedback of the ocean biosphere over this century.

As discussed there are a myriad of processes that could modify the C:N:P ratios of organic matter production and remineralization, with both negative and positive impacts on ocean carbon storage. However, inherent features of the ocean's carbon and nutrient cycles, as demonstrated by ocean carbon simulations appear unable to produce more than 50 Pg C change in carbon storage by the end of this century. Although these studies demonstrate the difficulty in trying to change the ocean carbon storage on less than a century time-scale, changes in the C:N:P ratios may have important consequences on the marine organisms and ecosystems. As discussed by [29••], an increase in the C:N ratio of exported organic matter [24••] increased the volume of anoxic water by 55% by the end of this century. An expansion of the anoxic regions would have detrimental impacts on ocean biota, and increase the decomposition of organic matter by denitrification, thereby reducing the nitrate pool in the ocean leading to a reduction in biological production and a preference for N-fixing phytoplankton [20]. Similarly, increased carbon export would also locally increase the carbon content of the ocean, this would accelerate the acidification of the ocean [28•] potentially amplifying marine ecosystem changes [27].

Conclusions

On both the land and in the ocean, the carbon and nutrient cycles are linked and this impacts the potential for the two biospheres to alter their ability to sequester carbon both now and in the future. The linkages between carbon and nutrients are quite different between land and ocean and these differences have significant implications on the time-scale of the carbon–nutrient–climate interactions.

On land most ecosystems are either N or P limited, therefore availability of N and P places an important constraint on the ability of the land biosphere to sequester carbon. The omission of N limitation reduces the negative carbon-climate feedback by up to 30% [5••]. The predicted increased N-deposition on land biosphere's subtropical regions coupled with increased N-fixation may shift nutrient limitation from N to P. Therefore, we postulate that P limitation will be important to further reducing land carbon-climate feedback. To quantify the future land carbon-climate feedback requires land carbon models that include the N and P cycles. The inclusion of the N and P cycles into land carbon models should be process based to allow for interactions between the N, P, and C cycles. Although there is uncertainty in the processes controlling these cycles both now and with future environmental change (e.g. N-fixation), enough is known to enable a revised estimate of the land carbon-climate feedback with combined carbon–nutrient models. Simulations with such models will also help identify the processes, which are most uncertain and could have the biggest impact on the future land carbon storage, and help direct where further process understanding is needed.

In the ocean, circulation primarily supplies nutrients and carbon to the ocean biota with nearly constant C:N:P ratios, unsurprisingly most biological uptake and remineralization occur with similar ratios. This in conjunction with the rapid recycling of carbon and nutrients by a low living biomass with high turnover rates make it difficult for biological processes with different nutrient utilization ratios to alter the carbon sequestered by the ocean on a century time-scale. Although these biological processes do not provide a large century-scale carbon-climate feedback, at longer time-scales they may have a large influence on atmospheric concentrations and therefore have a large carbon-climate feedback. The weak century-scale carbon-climate feedback of the ocean does not diminish the need to better understand the mechanisms controlling the C:N:P ratios. Indeed an improved mechanistic understanding of the processes controlling the C:N:P ratios of both the uptake and remineralization of organic matter is required to project the future impact of climate change on marine ecosystem composition and function.

Neither the land nor the ocean biosphere can be considered in isolation because they have compensating effects on the uptake of anthropogenic CO_2. A decrease in carbon uptake by the land biosphere due to nutrient limitation will increase the atmospheric CO_2 and increase the ocean uptake. The counteracting uptake response is purely a physical response of the ocean, and can reduce the land carbon cycle feedback by approximately 20% [2•]. A coupled earth system modelling approach that includes carbon and nutrient cycling on the land in ocean can determine the potential biosphere carbon-climate feedback. It can also be used to help assess the importance of different processes on carbon storage and identify where improved process understanding is needed.

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