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Nitrogen constraints on terrestrial carbon uptake: Implications for the global carbon-climate feedback

Ying-Ping Wang[1] and Benjamin Z. Houlton[2]

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[1] Carbon-climate feedback has been identified as one of the key areas of synthesis for the next Inter-governmental Panel on Climate Change (IPCC); however, most of the models on which the IPCC will rely are yet to consider vital interactions between nitrogen (N) and carbon (C) cycles. A major impediment to including N limitation in model predictions has been the lack of constraint to rates of N fixation worldwide. Here we use a theoretical framework that considers interactions of C and nutrients to estimate rates of terrestrial N fixation, and thereby examining how the constraints of N on land C uptake and global warming. We show that most global models without nutrient limitations significantly overestimated land C uptake, thus underestimating both the pace and magnitude of the predicted global warming. We suggest that the next IPCC assessment should consider nutrient constraints on carbon-climate feedback and the pace of global warming.

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1. Introduction

[2] Nitrogen (N) limits the productivity of many ecosystems globally, particularly those in extra-tropical terrestrial biomes and in recently disturbed (i.e., clearing, fire) tropical sites [*Vitousek and Howarth*, 1991]. This limitation occurs because the supply of soil mineral N is lower than plant N demands – as demonstrated by field experiments involving new N inputs, particularly N fertilizer inputs, which commonly stimulate net primary productivity (NPP) and terrestrial C storage [*van Groenigen et al.*, 2006]. Additionally, conceptual [e.g., *Luo et al.*, 2004], mass-balance [*Hungate et al.*, 2003] and numerical-simulation [*Thornton et al.*, 2007; *Sokolov et al.*, 2008] analyses have suggested that such widespread N limitation can significantly impact C uptake by the land biosphere and carbon-climate feedback. However, N fixation, the largest N input to the unmanaged land surface, is yet to be treated in a mechanistic manner, questioning the validity of these predictions and their global-scale implications. For example, N fixation is widely known to interact strongly with myriad controls – notably, light, C, nutrients and climate [*Houlton et al.*, 2008] – yet such controls have not been explicitly considered in past analyses. This study provides the first such spatially explicit estimate of N fixation on land, considering interactions between fixation, C, nutrients and climate, assessing the strength of carbon-climate feedback globally.

[3] Here we estimate N fixation (symbiotic and asymbiotic) and its responses to [CO_2] (C_a) and temperature change (ΔT_a) using a process-based model that explicitly accounts for the fundamental interactions between N fixation, nutrients, climate and other resources (e.g., light) [*Wang et al.*, 2007]. We then quantify the uncertainties in the amount of N required to store C for a range of N:C ratios among different C pools in the 11 models of the Coupled Carbon Cycle Climate Model Intercomparison Project (C4MIP) [*Friedlingstein et al.*, 2006]. Finally, we quantify a "global N deficit", defined as the difference between new N inputs and the amount of N needed to store the additional C simulated by the different models. Where the N deficit is negative (i.e., not enough N to store C), we identify the presence of "excess C" [*Sokolov et al.*, 2008]. After partitioning this "excess" C into oceanic and atmospheric sinks, we thus re-calculate the radiative forcing and increased global temperatures associated with the level of atmospheric [CO_2] enrichment.

2. Methods

[4] The amount of N available to store additional C depends on the partitioning of C into plant, litter and soil, the geographic distribution of their N:C ratios, and N inputs among different sectors of the terrestrial biosphere. To capture the broad spatial patterns of N inputs and N:C ratios in our analysis, we divide the global land biosphere into two regions: region 1 for tropical and subtropical region (30°S to 30°N) vs. region 2 for the rest.

[5] The N deficit (ΔN_i) for region i (i = 1, or 2) at time t is defined as the difference between the new N inputs available (N_a) and the N required to store the C as simulated by each of 11 models (N_r) from 1900 to t. That is

$$\Delta N_i(t) = \min\left(0, N_{a,i}(t) - N_{r,i}(t)\right) \qquad (1)$$

Our approach assumes that new inputs are requisite to changing the total terrestrial inventory of N above 1900 levels. This N is thus available to store additional C, and is calculated as the sum of the fraction (e) of N inputs via atmospheric N deposition ($N_{d,i}$) and N fixation (asymbiotic and symbiotic) ($N_{fix,i}$).

[6] N deposition was extrapolated over time using estimates of *Dentener* [2006] for the years 1860, 1993 and 2050 and fossil fuel emissions as based on the C4MIP simulations; asymbiotic N fixation was estimated under the present climate using the data compiled for different terrestrial biomes in the work by *Cleveland et al.* [1999]; and symbiotic

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[1] CSIRO Marine and Atmospheric Research and CAWCR, Aspendale, Victoria, Australia.

[2] Department of Land, Air and Water Resources, University of California, Davis, California, USA.

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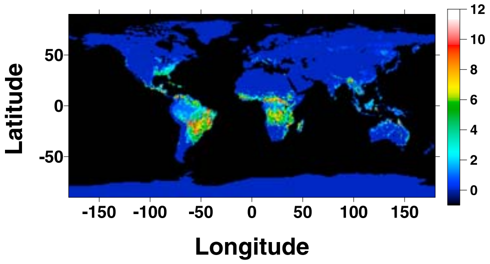

Figure 1. Model-based estimate of symbiotic N fixation (g N m^{-2} $year^{-1}$) over land under the present climate and preindustrial [CO_2] of 290 ppm. Area in black represents ocean or inland water.

N fixation was estimated using a model, CASACNP [*Wang et al.*, 2007; *Houlton et al.*, 2008]. The responses of both asymbiotic and symbiotic N fixation to increasing surface air temperature and atmospheric [CO_2] were estimated using CASACNP (see auxiliary material for further details).[1]

[7] The N required for storing additional C in plants and soils after 1900 is calculated as

$$N_{r,i}(t) = \Delta C_{p,i}(t) n_{p,i} + \Delta C_{l,i}(t) n_{l,i} + \Delta C_{s,i}(t) n_{s,i} \qquad (2)$$

where $n_{p,i}$, $n_{l,i}$ and $n_{s,i}$ are the N:C ratios of plant, litter and soil C pools, respectively; $\Delta C_{p,i}(t)$, $\Delta C_{l,i}(t)$ and $\Delta C_{s,i}(t)$ represent the increase in C in plant, litter and soil pools at year *t* relative to 1900, respectively. In some of the C4MIP models, litter was not treated independently of the soil. In these cases, we assumed that 40% of the total increase in C in soil was due to an increase in litter C, which is based on detailed estimates of litter and soil organic C pool dynamics from 1900 to 2100 by CSM-1.

[8] When $N_{a,i} > N_{r,i}$, the surplus N ($N_{a,i} - N_{r,i}$) is stored in plant or soil, and can be used to store additional C when needed. When $\Delta N_i(_t) < 0$, N supplies cannot adequately store the amount of C predicted by a given model at given C:N ratio. We partition the C that cannot be stored in the terrestrial biosphere, or "excess C", into the atmosphere and ocean, with global temperatures recalculated following the method outlined by *Friedlingstein et al.* [2006] for each model. Because $n_{p,i}$ is less than $n_{s,i,}$, it is possible that C storage can increase without additional N added to the system, particularly where the increase in plant C is larger than the decrease in soil C. To account for this effect, we estimated the N deficit and excess C across a reasonable range of $n_{p,i,}$ and $n_{s,i}$. Finally, because most models predict a peak in C uptake by terrestrial biosphere around year 2050, we focus our analysis on two periods, 1900 to 2050 and 1900 to 2099.

3. Results and Discussion

[9] We asked whether N inputs are substantial enough to satisfy the N requirements of C storage as simulated by the 11 C4MIP models (see Table S2 of the auxiliary material for the identity of all 11 models). Relative to 1900 levels, among the models, the amount of new C storage varies considerably, from between 28 Gt C to 414 Gt C by year 2050, to between 13 Gt C to 844 Gt C by year 2099. In all cases, more than 50% of the new C is stored in live terrestrial plant biomass (the remainder being stored in litter and soil). Using a range of N:C ratios for plant, litter and soil organic matter pools (see Methods), we thus estimate that the amount of N required to satisfy the storage of new C varies from 0 to 10.6 Gt N by 2050 and from 0 to 17.1 Gt N by 2099.

[10] Two models, FRCGC and UMD, require no new N inputs to store the amount of C estimated for 1900 to 2099. These models predict an increase in plant C and a decrease in soil and litter C; the amount of N required can be met entirely by the mineralization of soil organic matter. In all other case, however, new N is required to store the estimated amount of C, involving two primary paths – N_2 fixation and deposition. Here we examine the magnitude of such N inputs, and their capacity to satisfy the N demands of the terrestrial biosphere.

[11] Our best estimate of the global symbiotic N fixation flux using CASACNP is 0.125 Gt N for year 1900; this falls within the range of previous ones (0.11–0.29 Gt N $year^{-1}$) [*Cleveland et al.*, 1999], with tropical evergreen forest and savannah biomes accounting for 85% of the total symbiotic N fixation inputs (see Figure 1). Our model indicates that symbiotic N fixation is low in the extra-tropical zone (region 2) (~0.018 Gt N $year^{-1}$), matching global expectations for a strong latitudinal gradient in N fixation in the terrestrial biosphere [*Houlton et al.*, 2008]. We also estimate a global asymbiotic N fixation flux of 0.007 Gt N $year^{-1}$ over land under the present climate and preindustrial [CO_2] levels (290 ppmv). The total N fixation flux (symbiotic and free-living), is 0.13 Gt N $year^{-1}$ in region 1 and 0.02 Gt N $year^{-1}$ in region 2, and the fraction of N fixed asymbiotically is 17% in region 1 and 44% in region 2 in year 1900.

[12] To study the sensitivity of C sequestration to changes in N, we provide upper- and lower-bound estimates of N fixation owning to the diverging response of N fixation to elevated [CO_2] observed experimentally [*West et al.*, 2005]. The upper-bound is based on the nonlinear response of N fixation to increasing [CO_2] and temperature, whereas the lower-bound estimate is based solely on temperature (see Figure 2). Our modelled responses of N fixation to increasing [CO_2] and rising temperatures differ markedly from *Hungate et al.*'s [2003] analysis; they did not consider the fundamental temperature-sensitivity of nitrogenase and treated fixation as a linear function of increasing [CO_2]. Because N fixation

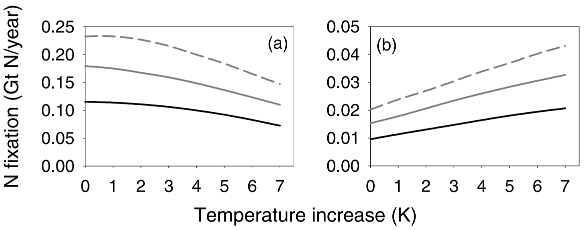

Figure 2. Modelled response of symbiotic N fixation to temperature increase and atmospheric [CO_2]. Results for (a) region 1 and (b) region 2 are shown for [CO_2] of 290 ppm (solid black line), 550 ppm (solid grey line) and 1000 ppm (dashed grey line).

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[1] Auxiliary materials are available in the HTML. doi:10.1029/2009GL041009.

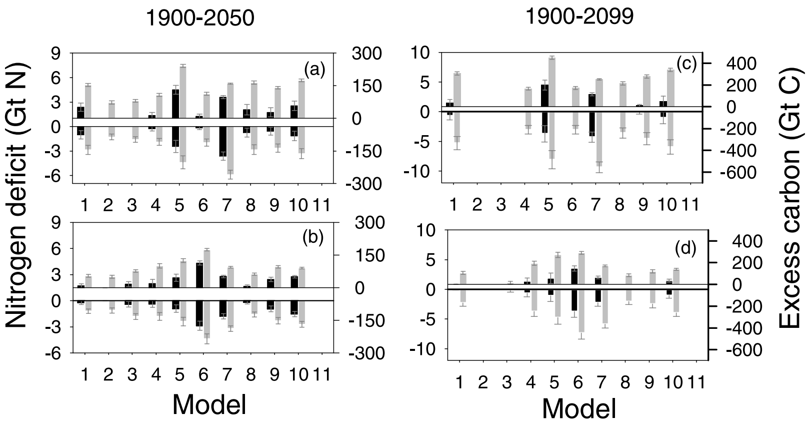

Figure 3. Nitrogen deficit (negative) and excess land carbon (positive) for the periods of (a, b) 1900 to 2050 and (c, d) 1900 to 2099. Figures 3a and 3c are for region 1 and Figures 3b and 3d are for region 2. The black and grey bars correspond to the nitrogen deficit or excess carbon for the upper and lower bounds of N fixation, respectively. The error bars represent the minimal and maximal values for the ranges of plant and soil N:C ratios and the fraction of N deposition available for C storage.

is energetically expensive and broadly C-limited, this CO_2-driven increase in NPP markedly enhances N fixation inputs in our upper-bound estimate of fixation (Figure 2; gray curves). While our model explicitly simulates P limitation to N fixation, it does not include those limitations associated with low trace element availabilities – particularly iron, vanadium or molybdenum. To simulate such effects, we assume that N fixation does not respond to increasing $[CO_2]$ at a given ΔT_a (black curves in Figure 2). This lower bound response seems to be consistent with field-based observations of transient increases in fixation with elevated $[CO_2]$, followed by down-regulation after a few years [*Hungate et al.*, 2004].

[13] Moreover, there are some significant differences between our estimates and those based on empirical proxies, particularly potential evapotranspiration (PET) [*Cleveland et al.*, 1999] or NPP [*Thornton et al.*, 2007]. First, both empirical models would predict a higher N fixation rate in tropical rainforests than in savannahs. In contrast, our model predicts higher rates of N fixation in the tropical savannah than tropical evergreen forest biomes. This is largely due to a more substantial energetic constraint to fixation in lowland tropical forests as opposed to savannahs, which have more open canopies and higher light penetration at the ground surface. In addition, our modelled distribution of symbiotic N fixation within the Amazon basin appears more consistent with field - based estimates of the abundance [*ter Steege et al.*, 2006] of putative fixers (i.e. legumes) than PET extrapolations [*Cleveland et al.*, 1999].

[14] More importantly, the predicted response of N fixation to temperature in our model is different from those of other models. For example, while empirically-based models would predict an increase in N fixation with T in both regions [*Cleveland et al.*, 1999], our model results indicate divergent responses of N fixation to temperature across extra-tropical vs. tropical regions. This is because current surface air temperature in region 1(tropics) is close to the optimal temperature [*Houlton et al.*, 2008] for fixing N, whereas the current surface air temperature is significantly below the optimal temperature for fixation in region 2 (extra-tropics). Therefore future surface warming will likely reduce N fixation in region 1 but increase N fixation in region 2.

[15] From 1900 to 2050, we find an upper limit of additional N fixation (both symbiotic and asymbiotic paths combined) that varies between 1.5 to 2.3 Gt N in region 1 and between 1.0 to 1.7 Gt N in region 2; the lower limit of additional N fixation is −0.1 to −0.17 Gt N in region 1 and 0.13 to 0.43 Gt N in region 2. Warming alone (i.e., no CO2 stimulation, the lower limit) reduces N availability in region 1 but increases N availability in region 2. The global net effect, depending the predicted warming pattern, is to increase overall global N availability and reduce the excess C as compared with the case when N fixation is kept constant after 1900 (see Table S2 of the auxiliary material). The upper limit of additional N fixation is 3.5 to 5.5 Gt N for region 1, or 2.9 and 4.3 Gt N for region 2 and the lower limit is −0.1 to −0.7 Gt N for region 1 and 0.4 to 0.9 Gt N for region 2 from 1900 to 2099.

[16] Finally, we estimate that the total amount of additional N deposition to the land surface is 3.4 Gt N from 1900 to 2050, or 7.1 Gt N from 1900 to 2099 globally, and is distributed about equally among regions 1 and 2. If as suggested only 7% to 17% of the deposited N is available for storing additional C globally (citation), the amount of the deposited N available for storing C is 0.24 to 0.58 Gt N from 1900 to 2050 and 0.5 to 1.2 Gt N from 1900 to 2099.

[17] Taken all together, we thus conduct an N supply – demand analysis, which points to a substantial deficit in N for most models under most conditions. Figure 3 shows the calculated N deficits (supplies – demands) for the two regions (see equation (1)). The error bar for each model represents the uncertainty in both the N input and the N required for storing additional C. Nine models overestimate terrestrial C storage (16 to 149 Gt of excess C) compared to our upper bound estimate of N fixation; if the lower bound is used, the predicted C storage seems unsustainable for all models except UMD by 2050. The N deficit becomes less negative, decreases from 2050 to 2099 in three models (FRCGC, HadCM3LC and UMD), as they predict a net release of C from land to the atmosphere from 2050 to 2099. The predicted increase in C pools by these three models can be met from the mineralization of organic matter without any additional N available from 1900 to 2099. Two

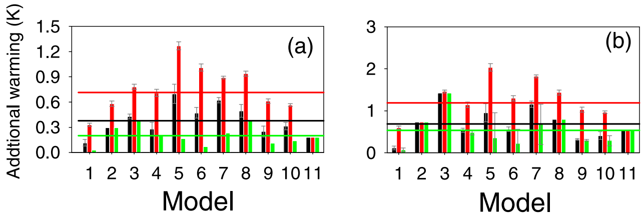

Figure 4. The additional warming owing to carbon-climate feedback as estimated by 11 different models in the C4MIP experiment (no N limitation considered; green bar) vs. the estimated additional warming when nitrogen limitation is considered (black for upper estimate and red for lower–bound estimates of N fixation). Lines represent the mean of the 11 models under the different scenarios (i.e., like colors correspond to bars). It is (a) for year 2050 and (b) for year 2099. The error bars represent the minimal and maximal additional warming for ranges of plant and soil N:C ratios and the fraction of N deposition available for C storage.

other models (LLNL and MPI) predict unabated rates of CO_2 uptake all the way to year 2099; the new N required to support C accumulation is 12.5 Gt N for model LLNL and 15.9 Gt N for model MPI according to our analysis, substantially beyond the upper limit of total new N inputs we estimated (i.e., 10.9 Gt N) (Figure 3). For models FRCGC and UMD, the estimated N required is lower than the amount of additional N available even in the absence of new N inputs between 1900 to 2099; these models may have underestimated land C uptake, since they assumes a very low CO_2 fertilization effect [*Friedlingstein et al.*, 2006].

[18] Finally, we examined the effect of N limitation on global climate warming, expressed as the net forcing of "excess C" (see Figure 3), which can not be stored on land; this C must enter either the atmosphere the ocean. We estimated the partitioning of excess C between atmospheric and oceanic sinks and the associated magnitudes of additional warming for each of the 11 models (see Figure 4). On average, the additional warming in the absence of N limitation varies from 0.20 K by 2050 to 0.54 K by 2099 [*Friedlingstein et al.*, 2006]. With explicit consideration of N limitation here, that magnitude of warming increases from 0.38 K to 0.72 K by 2050 and 0.69 to 1.19 K by 2099 – depending on the level of N fixation (high vs. low scenarios, respectively).

[19] In sum, our analysis, which is the first to consider C, N, P and biophysical (temperature, light) controls on fixation within the context of climate change, suggests that N limitation can significantly constrain the C uptake capacity of the land biosphere. The amount of warming that is associated with anthropogenic CO_2 emissions that can not be absorbed by natural land sinks is potentially substantial (Figure 4). This adds to a growing body of evidence for the importance of N in constraining CO_2 uptake and storage over land and the trajectory of the predicted warming by the end of this century [*Thornton et al.*, 2007; *Sokolov et al.*, 2008]. These results, if accurate, have significant implications for the magnitude of allowable emissions that will be required to stabilize global climate change, an emphasis of the next IPCC assessment [*Hibbard et al.*, 2007]: i.e., if C uptake by the land biosphere is increasingly more limited by available N and other nutrient resources, future warming will be more substantial and rapid than the current models suggest. Consequently, even more drastic reductions in CO_2 emissions will be necessary to stabilize the future climate.

4. Conclusions and Implications

[20] We draw two key conclusions from our study:

[21] 1. Warming increases N fixation at the middle and high latitudes, but reduces N fixation in low latitude tropical regions. The response of N fixation to increasing $[CO_2]$ contributes to most of the uncertainty in the amount of N available for storing carbon in the future.

[22] 2. Nitrogen limitation imposes a significant constraint to C uptake by terrestrial biosphere by 2099. Most of the fully coupled carbon climate models as reported by *Friedlingstein et al.* [2006] may have overestimated C uptake and underestimated the pace and magnitude of global warming. On average our estimated additional warming may vary between 0.38 K to 0.72 K by 2050 and 0.69 to 1.19 by 2099 when N limitation is considered.

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B. Z. Houlton, Department of Land, Air and Water Resources, University of California, One Shields Ave., Davis, CA 95616, USA.

Y.-P. Wang, CSIRO Marine and Atmospheric Research, Private Bag 1, Aspendale, Vic 3195, Australia. (yingping.wang@csiro.au)