MIT Joint Program on the Science and Policy of Global Change

Consequences of Considering Carbon/Nitrogen Interactions on the Feedbacks between Climate and the Terrestrial Carbon Cycle

Andrei P. Sokolov, David W. Kicklighter, Jerry M. Melillo, Benjamin Felzer,
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Report No. 151
June 2007

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To inform processes of policy development and implementation, climate change research needs to focus on improving the prediction of those variables that are most relevant to economic, social, and environmental effects. In turn, the greenhouse gas and atmospheric aerosol assumptions underlying climate analysis need to be related to the economic, technological, and political forces that drive emissions, and to the results of international agreements and mitigation. Further, assessments of possible societal and ecosystem impacts, and analysis of mitigation strategies, need to be based on realistic evaluation of the uncertainties of climate science.

This report is one of a series intended to communicate research results and improve public understanding of climate issues, thereby contributing to informed debate about the climate issue, the uncertainties, and the economic and social implications of policy alternatives. Titles in the Report Series to date are listed on the inside back cover.

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Abstract

A number of observational studies indicate that carbon sequestration by terrestrial ecosystems in a world with an atmosphere richer in carbon dioxide and a warmer climate depends on the interactions between the carbon and nitrogen cycles. However, most terrestrial ecosystem models being used in climate-change assessments do not take into account these interactions. Here we explore how carbon/nitrogen interactions in terrestrial ecosystems affect feedbacks to the climate system using the MIT Integrated Global Systems Model (IGSM) and its terrestrial ecosystems submodel, the Terrestrial Ecosystems Model (TEM). We use two versions of TEM, one with (standard TEM) and one without (carbon-only TEM) carbon/nitrogen interactions. Feedbacks between climate and the terrestrial carbon cycle are estimated by comparing model response to an increase in atmospheric CO_2 *concentration with and without climate change.*

Overall, for small or moderate increases in surface temperatures, the terrestrial biosphere simulated by the standard TEM takes up less atmospheric carbon than the carbon-only version, resulting in a larger increase in atmospheric CO_2 *concentration for a given amount of carbon emitted. With strong surface warming, the terrestrial biosphere simulated by the standard TEM may still become a carbon source early in the 23rd century.*

Our simulations also show that consideration of carbon/nitrogen interactions not only limits the effect of CO_2 *fertilization in the absence of climate change, but also changes the sign of the carbon feedback with climate change. In the simulations with the carbon-only version of TEM, surface warming significantly reduces carbon sequestration in both vegetation and soil, leading to a positive carbon-cycle feedback to the climate system. However, in simulations with standard TEM, the increased decomposition of soil organic matter with higher temperatures releases soil nitrogen to stimulate plant growth and carbon storage in the vegetation that is greater than the carbon lost from soil. As a result, sequestration of carbon in terrestrial ecosystems increases, in comparison to the fixed climate case, and the carbon cycle feedback to the climate system becomes negative for much of the next three centuries.*

Contents

1. INTRODUCTION

Carbon uptake by terrestrial ecosystems plays an important role in defining changes in the atmospheric CO_2 concentration and changes in climate. In turn, carbon uptake is influenced by these changes. It has long been recognized that nitrogen limitations often constrain carbon accumulations in mid- and high-latitude ecosystems, such as temperate and boreal forests (*e.g.*, Mitchell and Chandler 1939, Tamm *et al.*, 1982). Recent research on plant responses to elevated

CO_2 concentrations is also consistent with the idea that low nitrogen availability can constrain carbon sequestration in terrestrial ecosystems (Oren *et al.,* 2001; Luo *et al.* 2004, 2006; Reich *et al.*, 2006; Canadell *et al.,* 2007).

The possible impacts of changes in climate on the terrestrial ecosystem have been the subject of numerous studies carried out in recent years (*e.g.,* Friedlingstein *et al.*, 2006; Matthew, 2005; Plattner *et al.*, 2007). However, most of the terrestrial biosphere models currently used in climate change assessments, including the IPCC's Fourth Assessment, do not consider nitrogen limitations on net carbon storage. Thus, they probably exaggerate the terrestrial biosphere's potential to accumulate carbon and thereby slow the atmospheric CO_2 rise and the rate of climate change (Hungate *et al.,* 2003).

In addition, terrestrial biosphere models that ignore carbon-nitrogen interactions may also be misrepresenting the nature of the feedback between the land carbon cycle and the climate. In simulations with these models, warming reduces terrestrial carbon uptake resulting in a positive feedback to the climate system. In some cases, terrestrial ecosystems even switch from being a carbon sink to being a carbon source by the year 2100 (Cox *et al*., 2000). While warming will increase both plant and soil respiration, it will also result in additional soil nitrogen being made available to the vegetation as it increases soil organic matter decay (Peterjohn *et al*., 1994; Melillo, 1995, 2002). If this additional available nitrogen promotes more carbon storage in plants than is lost from soil respiration, warming will cause some biomes, including temperate and boreal forests, to exhibit an enhanced carbon sequestration (McGuire *et al*., 1992; Den Elzen *et al*., 1997).

In a recent model intercomparison (Plattner *et al*., 2007) of Earth system models of intermediate complexity (EMICs), the responses of terrestrial carbon dynamics simulated by the MIT Integrated Global System Model version 2 (IGSM 2, Sokolov *et al*., 2005) to future climate change are notably different from those of the other models. The MIT IGSM2 simulates a much weaker effect of CO_2 fertilization on terrestrial carbon uptake and simulates a negative feedback between the terrestrial carbon cycle and climate rather than a positive feedback as simulated by most other models. Although many variations in features among the EMICs may account for the differences in simulated responses, consideration of carbon/nitrogen interactions on terrestrial carbon dynamics is thought to be primarily responsible for the responses exhibited by the MIT IGSM2 in that study. In this study, we explore the consequences for the climate system of simulating the terrestrial biosphere with and without carbon/nitrogen interactions more directly. We use the MIT IGSM 2 and it's biogeochemistry submodel, the Terrestrial Ecosystem Model (TEM, Melillo *et al*., 1993; Felzer *et al*., 2004) with the carbon cycle either coupled to (standard TEM) or uncoupled from (carbon-only TEM) the nitrogen cycle. First, we carry out a set of simulations in which both the climate submodel of the IGSM and TEM are forced by prescribed changes in atmospheric CO_2 to evaluate the response of the different versions of TEM to changes in CO_2 and climate. Second, to analyze the consequences of carbon/nitrogen interactions on the projections of future climate change, we run the full version of the IGSM with an interactive carbon cycle that allows land and ocean carbon exchanges with the atmosphere in addition to prescribed anthropogenic emissions to influence simulated atmospheric composition and climate.

2. MODEL DESCRIPTION

The IGSM2 (Sokolov *et al*., 2005) is a fully coupled model of intermediate complexity of the Earth climate system that allows the simulation of critical feedbacks between submodels. The IGSM2.2 version used in this study includes the following components:

- An atmospheric dynamics, physics model,
- A mixed layer/anomaly-diffusive ocean model (ADOM) with carbon-cycle and sea ice submodels,
- A set of coupled land models, the Terrestrial Ecosystem Model (TEM), the Natural Emissions Model (NEM), and the Community Land Model (CLM), that encompass the terrestrial water and energy budgets and terrestrial ecosystem processes.

The time steps used in the various submodels range from 10 minutes for atmospheric dynamics to 1 month for TEM, reflecting differences in the characteristic timescales of the various processes simulated by the IGSM.

2.1 Atmospheric Dynamics and Physics

The MIT two-dimensional (2D) atmospheric dynamics and physics model (Sokolov and Stone 1998) is a zonally averaged statistical-dynamical 2D model that explicitly solves the primitive equations for the zonal mean state of the atmosphere and includes parameterizations of heat, moisture, and momentum transports by large-scale eddies based on baroclinic wave theory (Stone and Yao 1987 and 1990). The model's numerics and parameterizations of physical processes, including clouds, convection, precipitation, radiation, boundary layer processes, and surface fluxes, are built upon those of the Goddard Institute for Space Studies (GISS) GCM (Hansen *et al*., 1983). The version used in this study has a 4º resolution in latitude and 11 levels in the vertical dimension.

The MIT 2D atmospheric dynamics and physics model allows up to 4 different types of surfaces in each zonal band (ice free ocean, sea-ice, land, and land-ice). For each kind of surface, characteristics such as temperature, soil moisture, albedo, as well as turbulent and radiative fluxes, are calculated separately. The area-weighted fluxes from the different surface types are used to calculate the change of temperature, humidity, and wind speed in the atmosphere. The sensitivity of the atmospheric model to external forcing (S) can be changed by varying the cloud feedback (Sokolov and Stone 1998; Sokolov, 2006).

2.2 Ocean Component

The ocean component of the IGSM2.2 consists of a Q-flux model of an upper-ocean layer with horizontal resolution of 4º in latitude and 5º in longitude, and a 3000m deep anomaly diffusing ocean model (ADOM) beneath (Sokolov *et al.*, 2007). The upper-ocean layer is divided into two sub-layers that vary in thickness over the year, a mixed layer and a seasonal thermocline layer that exists between the bottom of the mixed layer and the top of the deep ocean layer. The mixed-layer depth is prescribed based on observations as a function of time and location (Hansen *et al.*, 1983). In contrast with conventional upwelling-diffusion models, diffusion ADOM is not applied to temperature itself, but to the temperature difference from its values in a present-day climate simulation. The spatial distribution of the diffusion coefficients used in the diffusive model is based on observations of tritium mixing into the deep ocean (Hansen *et al.*, 1984).

A thermodynamic ice model is used for representing sea ice. This model has two ice layers and computes ice concentration (the percentage of area covered by ice) and ice thickness.

The 2-dimensional ocean carbon model used in the current version of the IGSM2.2 is described in Sokolov *et al.* (2007). It has sensitivity to changes in both CO_2 and climate that are similar to the sensitivities of other ocean carbon models (*e.g.*, Plattner *et al.*, 2007).

2.3 Land and Vegetation Processes

Within the IGSM2.2, land processes are represented with a Global Land System (GLS) framework (**Figure 1**) in which water and energy dynamics are simulated by the Community Land Model (CLM, Bonan *et al.*, 2002; Zeng *et al.*, 2002) and terrestrial carbon and nitrogen dynamics are simulated by the Terrestrial Ecosystem Model (TEM, Melillo *et al.*, 1993; Felzer *et al.*, 2004). The CLM provides TEM with estimates of evapotranspiration rates, soil moistures and soil temperatures for a mosaic of land cover types found within a 4° latitudinal band (Schlosser *et al.*, 2007). In TEM, the uptake of atmospheric carbon dioxide by vegetation, also known as gross primary production or GPP (**Figure 2**), is dependent upon photosynthetically active radiation (PAR), leaf phenology, air temperature, evapotranspiration rates, atmospheric concentrations of carbon dioxide and ozone, the availability of inorganic nitrogen in the soil, and the ratio of carbon to nitrogen (C:N) of new plant biomass (Raich *et al.*, 1991; McGuire *et al.*, 1997; Tian *et al.*, 1999; Felzer *et al.*, 2004). Carbon dioxide is released back to the atmosphere from terrestrial ecosystems as a result of the autotrophic respiration (R_A) of plants and the

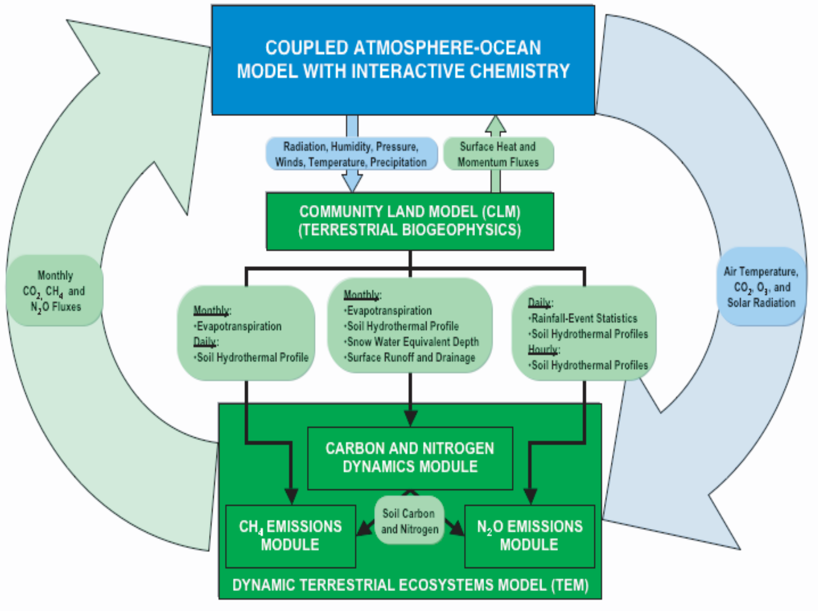

Figure 1. Global Land System (GLS) framework.

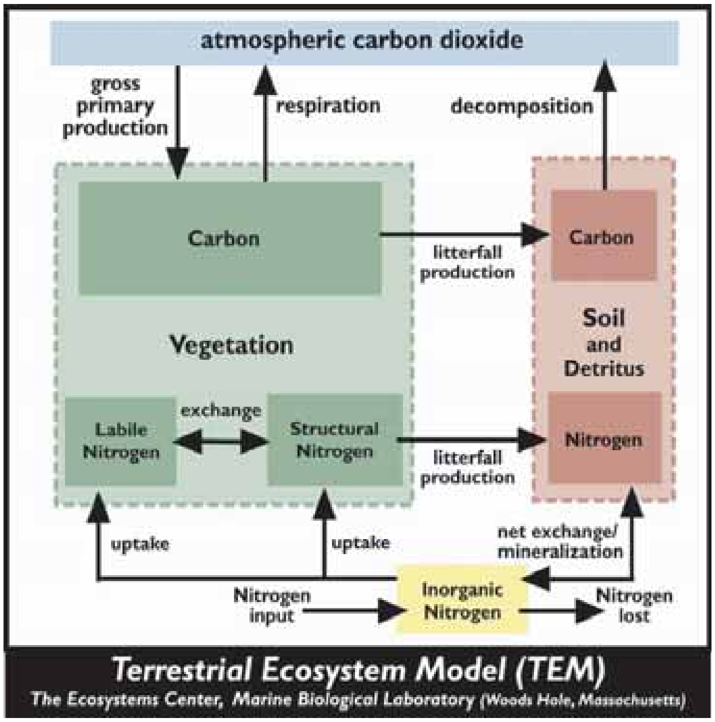

Figure 2. The Terrestrial Ecosystem Model (TEM). The state variables are: carbon in vegetation (CV); structural nitrogen in vegetation (NVS); labile nitrogen in vegetation (NVL); organic carbon in soils and detritus (CS); organic nitrogen in soils and detritus (NS); and available soil inorganic nitrogen (NAV). Arrows show carbon and nitrogen fluxes: GPP, gross primary productivity; RA, autotrophic respiration; RH, heterotrophic respiration; LC, litterfall carbon; LN, litterfall nitrogen; NUPTAKES, N uptake into the structural N pool of the vegetation; NUPTAKEL, N uptake into the labile N pool of the vegetation; NRESORB, N resorption from dying tissue into the labile N pool of the vegetation; NMOBIL, N mobilized between the structural and labile N pools of the vegetation; NETNMIN, net N mineralization of soil organic N; NINPUT, N inputs from the outside of the ecosystem; and NLOST, N loss from the ecosystem.

heterotrophic respiration (R_H) associated with the decomposition of soil organic matter. Plant respiration includes both maintenance respiration (R_M), which is dependent upon the amount of vegetation biomass and air temperature, and growth respiration, which is assumed to consume 20% of the available photosynthate (*i.e.* the difference between GPP and R_M) to construct new plant tissues. Net primary production (NPP), which is an important source of food and fiber for humans and other organisms on earth, is the net uptake of atmospheric carbon dioxide by plants and is calculated as the difference between GPP and R_A. Heterotrophic respiration depends upon the amount of soil organic matter, the C:N ratio of the soil organic matter, air temperature and soil moisture (Raich *et al.*, 1991; McGuire *et al.*, 1997; Tian *et al.*, 1999). Within an ecosystem, carbon may be stored either in vegetation biomass or in detritus (*i.e.* litter, standing dead and soil organic matter). In TEM, the carbon in vegetation biomass and detritus are each represented by a single pool (Figure 2). The transfer of carbon between these two pools is represented by litterfall carbon (L_C), which is calculated as a proportion of vegetation carbon. Changes in vegetation carbon (ΔVEGC, also known as biomass increment), detritus (ΔSOILC) and terrestrial carbon (ΔTOTALC) are then determined as a linear combination of these fluxes:

$$\Delta VEGC = GPP - R_A - L_C \tag{1a}$$

$$\Delta VEGC = NPP - L_C \tag{1b}$$

$$\Delta SOILC = L_C - R_H \tag{2}$$

$$\Delta TOTALC = \Delta VEGC + \Delta SOILC \tag{3a}$$

$$\Delta TOTALC = NPP - R_H \tag{3b}$$

Carbon sequestration in terrestrial ecosystems can be estimated by the GLS either as the sum of the estimated changes in carbon in vegetation and detritus (Equation 3a) or by the difference between NPP and R_H (Equation 3b), which is also known as net ecosystem production or NEP.

An important feature of TEM is that the model simulates the influence of terrestrial nitrogen dynamics on terrestrial carbon dynamics. First, the uptake of carbon dioxide by plants is assumed by TEM to be limited by nitrogen availability in most land ecosystems on earth. Tropical forests are the only exceptions, where nitrogen availability is not assumed to limit GPP under contemporary conditions. The nitrogen limitation is imposed by determining the ratio of an initial estimate of NPP to an initial estimate of the amount of inorganic nitrogen acquired by plants from the soil (NUPTAKE) plus the amount of vegetation labile nitrogen mobilized (NMOBIL) during a particular month (Pan *et al.*, 1998; Tian *et al.*, 1999). This NPP:(NUPTAKE+NMOBIL) ratio is then compared to a target C:N ratio for the production of new plant tissues (P_{CN}). If the NPP:(NUPTAKE+NMOBIL) ratio is greater than P_{CN}, then NPP is reduced to equal the multiplicative product of P_{CN} and the sum of NUPTAKE and NMOBIL because nitrogen is limiting. As experimental studies (McGuire *et al.*, 1995, Cotrufo *et al.*, 1998; Curtis and Wang, 1998; Norby *et al.*, 1999) have shown that plant tissue nitrogen concentrations change with enhanced CO_2 concentrations, we adjust P_{CN} with increasing atmospheric CO_2 concentrations to be consistent with the assumption of a linear 15% decrease in plant tissue nitrogen concentrations associated with a 340 ppmv increase in atmospheric CO_2 (McGuire *et al.*, 1997). Thus, vegetation biomass will contain more carbon per gram nitrogen under enhanced atmospheric CO_2 concentrations than under current conditions in our simulations. Second, TEM assumes that nitrogen availability in ecosystems is dependent upon the release of inorganic nitrogen from soil organic matter during decomposition (*i.e.* net nitrogen mineralization). This nitrogen is then available for uptake by plants to support plant productivity. If decomposition increases, perhaps as a result of higher temperatures, then more inorganic nitrogen is released and plant productivity may increase. Conversely, if decomposition decreases, plant productivity may decline due to increased nitrogen limitations. Thus, the recycling of nitrogen by decomposition plays an important role in the ability of plants to respond to changing environmental conditions in the TEM simulations (McGuire *et al.*, 1997; Xiao *et al.*, 1997, 1998; Pan *et al.*, 1998; Kicklighter *et al.*, 1999). While other models may implicitly account for the influence of nitrogen limitations on GPP with approaches such as the use of “biome-specific growth factors” (*e.g.*, Alexandrov *et al.*, 2003), these models do not account for the influence of potential changes in nitrogen availability associated with future climate change. Although the structure of TEM allows consideration of nitrogen inputs and losses from terrestrial ecosystems, no nitrogen is assumed to be added or lost from terrestrial ecosystems to influence nitrogen availability in the version of TEM used in the IGSM2. Thus, the total amount of nitrogen within an ecosystem does not change over a simulation, but nitrogen can be redistributed between vegetation and soils.

To examine the importance of this nitrogen recycling on carbon dynamics, TEM has been constructed such that the model can be run under "carbon-only" assumptions, where the amount of soil inorganic nitrogen is not allowed to change and plant productivity is not limited by nitrogen availability. In a previous study (Kicklighter *et al.*, 1999), nitrogen availability has been shown to greatly constrain the response of terrestrial ecosystems to potential enhanced atmospheric carbon dioxide concentrations in the future under a fixed climate. Indeed, in that study, the elimination of nitrogen constraints in the "carbon-only" version of TEM allowed a rate of carbon sequestration that was much greater than that normally obtained by other terrestrial carbon models under similar conditions. The rather large response is a result of using the same value (400 ppmv CO_2) for the Michaelis-Menten half saturation constant, which describes the effect of atmospheric carbon dioxide on GPP (McGuire *et al.*, 1992; Pan *et al.*, 1998), for the "carbon-only" version of TEM as in our standard "nitrogen limited" TEM. If we reduce the Michaelis-Menten half saturation constant to 150 ppmv CO_2 in the "carbon-only" version of TEM, we obtain simulated responses of ecosystems to enhanced atmospheric carbon dioxide concentrations that are similar to other terrestrial carbon models used in the IPCC's Fourth Assessment Report (Plattner *et al.*, 2007).

To estimate carbon fluxes from terrestrial ecosystems to the atmosphere, TEM is run for every land cover type in a mosaic established for each 4° latitudinal band used by the atmospheric dynamics and physics/chemistry model (Schlosser *et al.*, 2007). While air temperature, PAR and atmospheric concentrations of carbon dioxide and ozone are assumed to be the same for each land cover type in a latitudinal band, a provision is made to account for the varying precipitation amounts falling on ocean and land as well as across the various land cover types within each latitudinal band (Schlosser *et al.*, 2007). Thus, the GLS is able to represent some of the longitudinal variability across a 4° latitudinal band that influences evapotranspiration, soil moisture and terrestrial carbon dynamics, but is not able to represent any changes in longitudinal variability that may occur with climate change. The TEM results are area-weighted to obtain aggregate fluxes from each latitudinal band (Sokolov *et al.*, 2005). In the IGSM2.2, the TEM estimates carbon fluxes from only natural ecosystems. The influence of human disturbances on terrestrial carbon dynamics is currently determined by another model within the IGSM and these effects are not included in the analyses presented in this paper.

3. SIMULATIONS WITH PRESCRIBED CHANGES IN ATMOSPHERIC CO_2 CONCENTRATION

In the simulations described in this section, the atmospheric submodel of the IGSM is forced by prescribed changes in atmospheric CO_2 between year 1861 and year 2300 according to the IPCC scenario SP1000 (**Figure 3a**). Four simulations (**Table 1**) are carried out with the standard

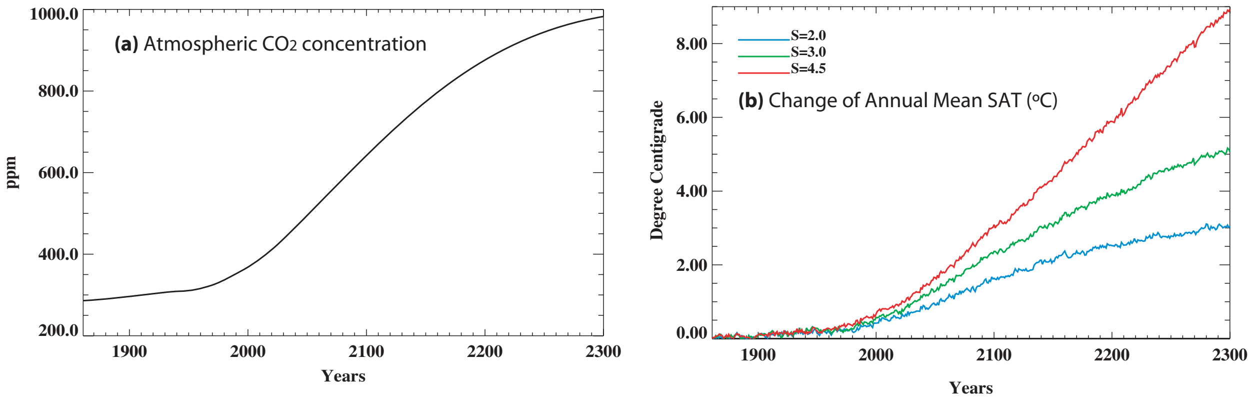

Figure 3. **(a)** SP1000 atmospheric CO_2 concentration, and **(b)** changes in surface air temperature in simulations with SP1000 scenario for different values of climate sensitivity.

Table 1. Simulations with SP1000 scenario with different versions of TEM.

Simulation	TEM version	Climate sensitivity	Carbon/nitrogen interactions considered?
CO_FF	Carbon-only	Fixed forcing	No
CO_2.0	Carbon-only	2.0 K	No
CO_3.0	Carbon-only	3.0 K	No
CO_4.5	Carbon-only	4.5 K	No
NL_FF	Standard	Fixed forcing	Yes
NL_2.0	Standard	2.0 K	Yes
NL_3.0	Standard	3.0 K	Yes
NL_4.5	Standard	4.5 K	Yes

and carbon-only versions of TEM, with a value of the Michaelis-Menten half saturation constant (*kc*) equal to 150 ppmv is used in both versions of TEM in these simulations. In the first simulation, changes in CO_2 concentration do not affect climate simulated by the atmospheric submodel. Therefore, TEM is forced by increasing CO_2 with climate corresponding to the initial atmospheric CO_2 concentrations. Following the terminology used in previous studies (*e.g.*, Friedlingstein *et al.*, 2006; Matthew, 2005; Plattner et al, 2007), we refer to this simulation as an "uncoupled simulation". In three "coupled" simulations, changes in climate are projected using three different values of model sensitivity (S, see section 2.1) corresponding to equilibrium surface warming of 2 K, 3 K and 4.5 K in response to the doubling of atmospheric CO_2 concentration. Changes in surface air temperature (SAT) produced in these latter simulations are shown in Figure 3b. The absence of feedbacks between terrestrial carbon uptake and atmospheric CO_2 concentration in these simulations allows us to compare the responses of the different versions of TEM to identical changes in atmospheric CO_2 concentrations alone and with changes in climate[1].

In this section, we first examine how carbon/nitrogen interactions influence the simulated response of terrestrial ecosystems to CO_2 fertilization and global warming. We then examine how our results compare to similar results of models used in the IPCC Fourth Assessment

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[1] We have carried out a set of sensitivity simulations, which showed that changes in precipitation have much smaller effect on terrestrial carbon cycle than changes in surface air temperature. Therefore we will only discuss impact of temperature increase.

Report. Finally, to examine how CO_2 fertilization assumptions influence simulated terrestrial source/sink behavior, we conduct additional simulations with the standard TEM, but use *kc* values equal to 400 ppmv and 700 ppmv, respectively.

3.1 Influence of Carbon/Nitrogen Interactions on the Simulated Response of Terrestrial Ecosystems to CO_2 Fertilization and Global Warming

The rate of CO_2 fertilization estimated for the carbon-only TEM with *kc* =150 is very close to the rate estimated for the Bern model (Plattner *et al.*, 2007). As a result, changes in terrestrial carbon stocks in the uncoupled simulations with the carbon-only TEM and the Bern model are also very close (**Figure 4**). Response of the carbon-only TEM to global warming is similar in pattern but somewhat larger than the response produced by the Bern model or most other terrestrial carbon models (Friedlingstein *et al.*, 2006). The behavior of the carbon-only TEM, resembles that of the Hadley Center model (Cox *et al.*, 2000), in that the terrestrial biosphere stops absorbing carbon when surface warming reaches a threshold. In simulations with the carbon-only TEM, this threshold occurs with a 4.5º C increase in global mean SAT around year 2150 in the S=4.5 K simulation and around year 2240 in the S=3 K simulation. For a different scenario of CO_2 increase, the corresponding temperature threshold is likely to be different.

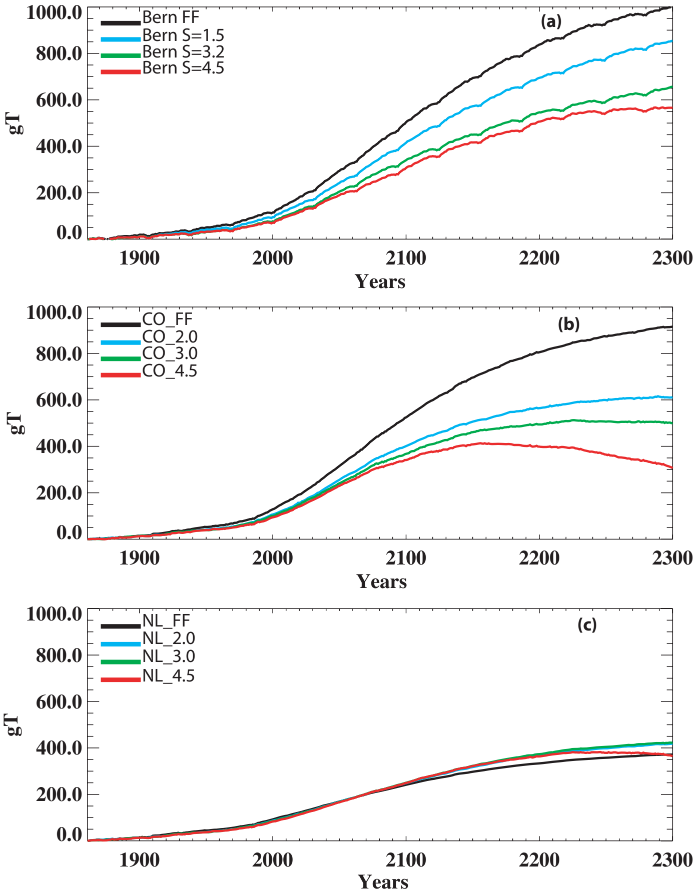

Figure 4. Changes in the terrestrial carbon simulated by **(a)** the Bern model, **(b)** carbon only TEM, and **(c)** standard TEM.

In contrast, changes in future total terrestrial carbon stocks in vegetation and soils projected by our standard “nitrogen-limited” TEM are much lower than those simulated by either the Bern model or the carbon-only TEM. In the uncoupled simulation, the standard TEM estimates a gain in terrestrial carbon storage that is only about 40% of the gain projected by the Bern model or the carbon-only TEM. In addition, consideration of carbon/nitrogen interactions changes the simulated response of these ecosystems to warming. In the Bern and carbon-only TEM simulations, which do not consider carbon/nitrogen interactions, warming causes less carbon to be stored in terrestrial ecosystems, a positive feedback, whereas in the standard “nitrogen-limited” TEM simulation, warming causes more carbon to be stored in terrestrial ecosystems, a negative feedback. However, as the SAT continues to increase, a temperature threshold may be reached when the negative feedback becomes positive. Thus, when SAT rises by about 6.5^{o} C around year 2220 in the standard TEM simulation with S = 4.5 K, the terrestrial biosphere becomes a carbon source.

It is worth noting that the carbon-only TEM estimates that the terrestrial biosphere accumulates more carbon than the standard TEM with the exception of the simulation with the largest temperature increases. While the standard TEM estimates that carbon storage in the terrestrial biosphere increases by 25 to 29% from the year 1861 to 2300, the carbon-only TEM estimates that this carbon storage increases by 25 to 74% depending on the degree of concurrent warming that occurs (**Table 2**).

The differences in the responses of carbon storage estimated by the two versions of TEM to changes in both atmospheric CO_2 and climate are largely the result of the differences in the carbon stored in vegetation. In the carbon-only TEM simulations, vegetation carbon increases by 53 to 77% from 1861 to 2300 (Table 2) with the accumulation of vegetation biomass becoming slower with additional warming (**Figure 5**a) as a result of enhanced plant respiration. In contrast, the standard TEM simulations estimate increases of vegetation carbon of only 12 to 41% between 1861 and 2300 (Table 2) with biomass accumulation becoming more rapid with additional warming (Figure 5b) as a result of enhanced nitrogen availability, which supports higher rates of plant productivity. Changes in the soil carbon simulated by the carbon-only and standard versions of TEM are qualitatively similar (Figures 5c and 5d), but differ in the strength of the response to CO_2 fertilization and warming. In the standard TEM simulations, carbon

Table 2. Changes in the amount of carbon stored in vegetation, soils and the terrestrial biosphere between 1861 and 2300 (expressed as the ratio to corresponding initial value) in the carbon-only (CO) and standard TEM (NL) simulations.

Simulation	ΔVEGC	ΔSOILC	ΔTOTALC
CO_FF	1.77	1.71	1.74
CO_2.0	1.63	1.32	1.50
CO_3.0	1.59	1.15	1.41
CO_4.5	1.53	0.87	1.25
NL_FF	1.12	1.40	1.25
NL_2.0	1.25	1.32	1.29
NL_3.0	1.33	1.25	1.29
NL_4.5	1.41	1.06	1.25

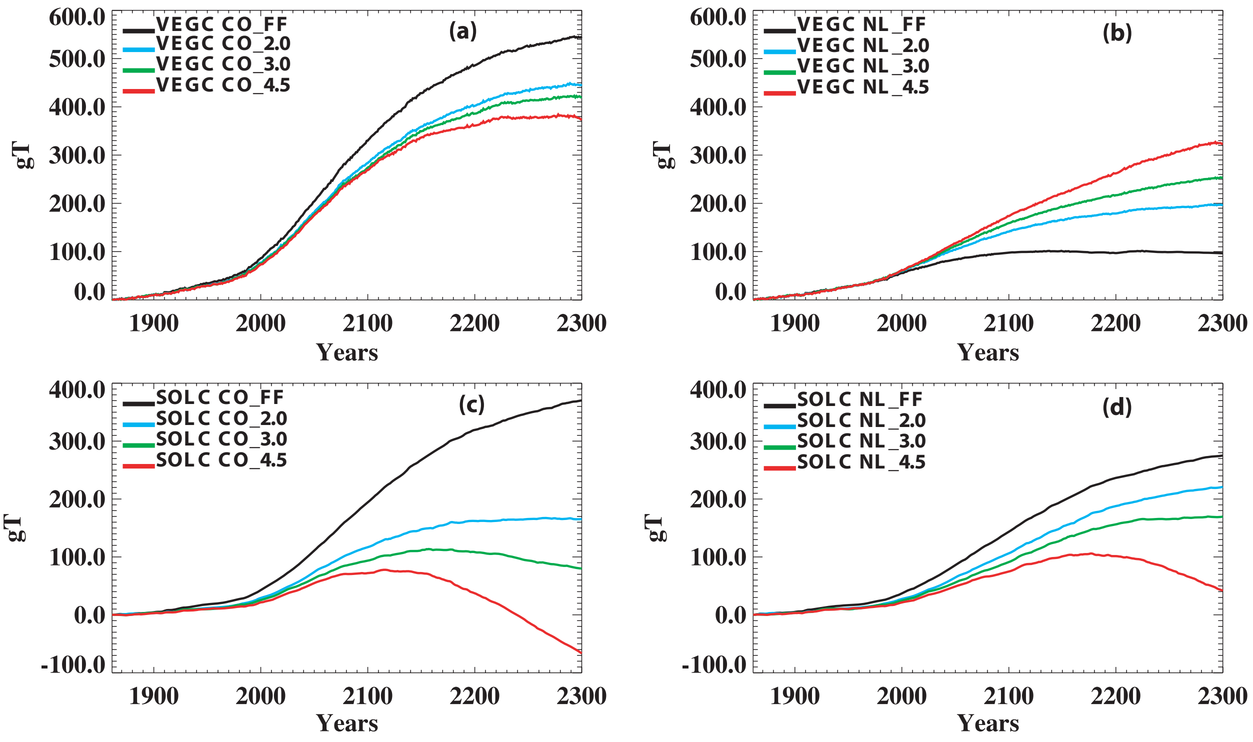

Figure 5. Changes in the vegetation **(top row)** and soil **(bottom row)** carbon simulated by the carbon only **(left column)** and standard TEM **(right column)**.

storage in soils increases by 6 to 40% between 1861 and 2300 with less carbon being stored under warmer climate conditions (Table 2) as a result of enhanced decomposition rates. In the carbon-only TEM simulations, the response is larger and ranges from a 13% loss of soil carbon under the warmest conditions to a 71% gain of soil carbon under fixed-forcing conditions. Additional details of how carbon/nitrogen interactions influence terrestrial carbon storage and fluxes between these two versions of TEM are given in the Appendix.

3.2 Comparisons to Other Studies

Different terrestrial biosphere models are often compared in terms of carbon uptake sensitivities to increases in atmospheric CO_2 and surface warming (Friedlingstein *et al.*, 2006, Plattner *et al.*, 2007). In these comparisons, it is assumed that the change in terrestrial carbon (ΔC) can be approximated by a linear function of the changes in CO_2 (ΔCO_2) and surface temperature ($\Delta Tsrf$),

$$\Delta C=\beta_L\ \Delta CO_2+\gamma_L\ \Delta Tsrf,$$

where the sensitivity to CO_2 (β_L) can be calculated from the change in terrestrial carbon in the uncoupled simulations ($\Delta Cunc$), as:

$$\beta_L=\Delta Cunc/\ \Delta CO_2,$$

and the sensitivity to surface temperature (γ_L) can be calculated from the change in terrestrial carbon from both the uncoupled simulation ($\Delta Cunc$), and a coupled simulation ($\Delta Ccou$), as:

γ_L=(ΔCcou- ΔCunc)/ ΔTsrf.

Both β_L and γ_L derived from the carbon-only TEM simulations (**Table 3**) fall in the ranges of values calculated with other terrestrial models (Friedlingstein *et al.*, 2006, Plattner *et al.*, 2007). As expected, β_L for the standard TEM is about 2.5 times smaller than for the carbon-only TEM as a result of nitrogen limitations on plant productivity. In addition, the standard TEM results provide positive values of γ_L, indicating enhanced carbon uptake with temperature, rather than the negative values of the carbon-only TEM results or the other models. For both versions of the TEM, sensitivity of carbon uptake to surface temperature (measured by absolute value of γ_L) decreases with the increase of the model climate sensitivity, suggesting a saturation of the temperature effect on carbon uptake. Since changes in the terrestrial carbon can only be roughly approximated by a linear function, both β_L and γ_L depend on time period. Values shown in table 3 are calculated using data from 1861 to 2300.

3.3 Sensitivity of Terrestrial Source/Sink Behavior to CO_2 Fertilization Assumptions

Simulated responses of the terrestrial biosphere to changes in CO_2 and climate also depend on the assumed rate of CO_2 fertilization. A *kc* value of 150 is at the low end of the range of values determined from laboratory and field studies (Raich *et al.*, 1991; McGuire *et al.*, 1992; Gunderson and Wullschleger, 1994; Curtis and Wang, 1998; Norby *et al.*, 1999, 2005). To evaluate this dependence we carried out additional simulations with the standard TEM for *kc* values of 400 ppmv and 700 ppmv. A change in the CO_2 fertilization rate has little impact on the model sensitivity to enhanced CO_2 concentrations; the value of β_L for the standard nitrogen-limited TEM does not depend on *kc*. It does, however, affect the strength of the carbon cycle/climate feedback; $\gamma_{L,}$ which increases with the rate of CO_2 fertilization. An increase in *kc* also increases the magnitude of surface warming at which the terrestrial biosphere switches from being a carbon sink to becoming a carbon source. In simulations with the standard TEM when *kc* equals either 400 ppmv or 700 ppmv, the terrestrial biosphere starts to be a source of atmospheric CO_2 rather than a sink when SAT rises by more than 11.5° C and 13° C respectively.

Table 3. Terrestrial carbon sensitivities to CO_2 (β_L) and surface warming (γ_L) at different climate sensitivities (2.0 K, 3.0 K or 4.5 K) for carbon-only (CO) and standard TEM (NL) simulations.

	β_L (Gt C ppm^{-1})	γ_L (Gt C K^{-1}) 2.0 K	3.0 K	4.5 K
CO_150	1.33	-99	-81	-69
NL_150	0.51	16	12	4
NL_400	0.53	25	20	15
NL_700	0.53	26	22	17

4. SIMULATIONS WITH AN INTERACTIVE CARBON CYCLE AND PRESCRIBED ANTHROPOGENIC EMISSIONS

To evaluate the impact of different treatments of carbon/nitrogen interactions on projections of future climate, we conduct a set of simulations using the IGSM2.2 with an interactive carbon cycle. In these simulations, atmospheric CO_2 concentrations are calculated using prescribed anthropogenic carbon emissions and simulated atmospheric exchanges of CO_2 with the land and the ocean. Similar to the protocol in Section 3, four simulations (one uncoupled and three coupled) are carried out with each version of the TEM. Because the effects of the simulated terrestrial and oceanic carbon uptake on the predicted atmospheric CO_2 concentrations and climate change depend on the magnitude of anthropogenic emissions, we carry out simulations using two emission scenarios, namely the Bern SP1000 and SP550 scenarios (see Plattner *et al.*, 2007).

Consideration of carbon/nitrogen interactions in terrestrial ecosystems has a large influence on the feedbacks between climate and carbon cycle. Because both the carbon-only TEM and the ocean carbon model, similar to other ocean carbon models, simulate positive feedbacks with climate, atmospheric CO_2 concentrations are estimated to increase (**Figure 6**) with the increase in surface warming associated with an increase in climate sensitivity. In contrast, a feedback between climate and the carbon cycle appears to be practically absent in the simulations with the standard TEM (Figure 6). The climate-related increase in terrestrial carbon uptake is compensated for by the decrease in the uptake by the ocean so that atmospheric CO_2 concentrations are almost identical in all simulations with the standard version of the TEM. It is worth noting that, in spite of the climate-change related decrease in terrestrial carbon uptake, the final atmospheric CO_2 concentrations in all of the SP500 simulations (Figure 6b) and in three out of four SP1000 simulations (Figure 6a) with the carbon-only TEM are lower than the standard TEM simulations in which terrestrial uptake of carbon is limited by nitrogen availability. The only exception is a simulation with SP1000 emissions and climate sensitivity of 4.5 K, where atmospheric CO_2 concentration becomes higher than in the corresponding simulation with the standard TEM only after year 2240. As a result, SAT increases more in all simulations using the standard TEM (**Figure 7**). The differences in simulated responses between the two TEM versions are more noticeable in the simulations using lower anthropogenic carbon emissions (Figures 6b and 7b). Therefore, accounting for terrestrial carbon/nitrogen dynamics is especially important for estimating climate impacts of different economic policies aimed to stabilization of the greenhouse gases concentrations in the atmosphere.

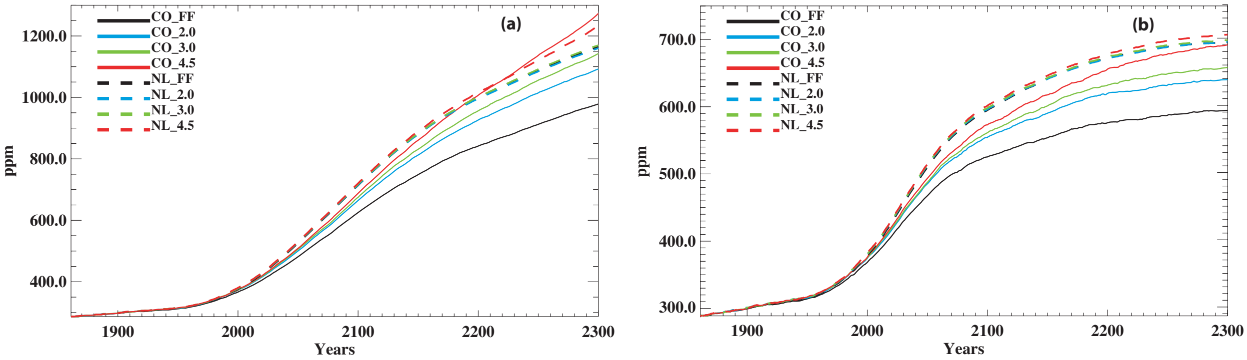

Figure 6. Atmospheric CO_2 concentrations obtained in simulations with SP1000 **(a)** and SP500 **(b)** emissions scenarios with TEM_CO (solid lines) and TEM_NL (dashed lines).

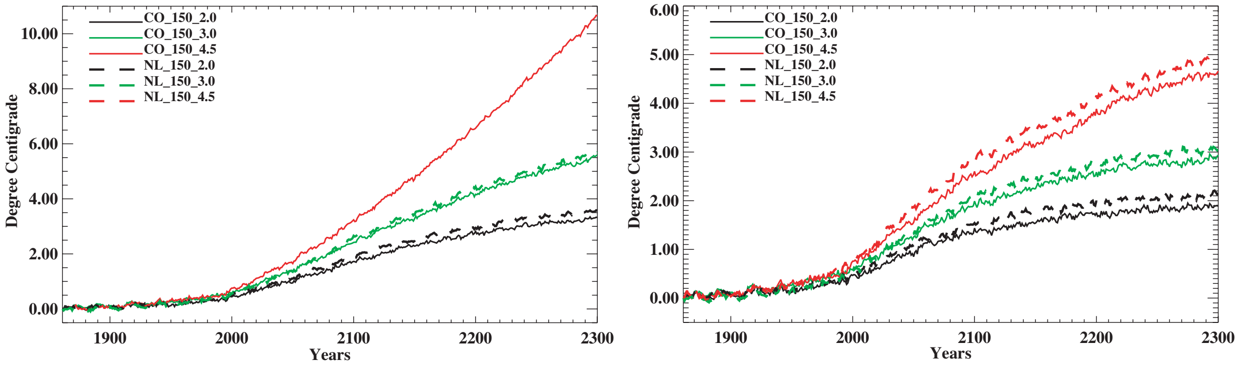

Figure 7. Changes in surface air temperature in simulations with SP1000 **(a)** and SP500 **(b)** emissions scenarios with TEM_CO (solid lines) and TEM_NL (dashed lines).

5. CONCLUSIONS.

Similar to the findings of McGuire *et al.* (1992) and den Elzen *et al.* (1997), the results of the simulations presented here indicate that consideration of the interactions between the carbon and nitrogen cycles significantly affect the response of the terrestrial biosphere to increases in atmospheric CO_2 concentration and surface air temperature. In addition, carbon/nitrogen interactions also affect the influence of the terrestrial biosphere on future atmospheric CO_2 concentrations and the earth's surface temperatures. On one hand, the limitation of carbon uptake by nitrogen availability significantly reduces the effect of CO_2 fertilization in the absence of surface warming. Thus, the standard TEM estimates a much smaller increase in terrestrial carbon uptake in the uncoupled simulations than in the analogous simulation with the carbon-only TEM. On the other hand, an increase in the surface temperature associated with elevated CO_2 concentrations increases the availability of nitrogen through mineralization of organic matter by increasing the decomposition of detritus. The elevated nitrogen availability, in turn, alleviates the nitrogen constraints on plant productivity in nitrogen-limited ecosystems such as boreal and temperate forests, amplifying the effect of the CO_2 increase on GPP. Because the C:N ratios for vegetation, particularly woody tissues, are significantly higher than those for soil organic matter, climate-change related increases in vegetation carbon can exceed the loss of soil carbon through enhanced decomposition to sequester carbon in terrestrial ecosystems (Melillo *et al.*, 2002). Thus, the standard TEM estimates more carbon will be sequestered in the coupled simulations than in the uncoupled simulations with a fixed climate. Without consideration of such carbon/nitrogen interactions, the carbon-only TEM estimates less carbon will be sequestered in the coupled simulations than in the uncoupled simulations. Due to such differences in the responses to changes in CO_2 and climate, the amount of atmospheric carbon sequestered by the terrestrial biosphere is quite different and the feedbacks between climate and the terrestrial carbon cycle simulated by two versions of TEM have different signs.

The impact of carbon/nitrogen interactions on the projected increase in atmospheric CO_2 depends, for given set of carbon emissions, on the climate characteristics defining the response of climate system to external forcing (*e.g.*, climate sensitivity or the rate of heat uptake by the ocean). In most cases, the terrestrial biosphere as simulated by the standard TEM absorbs less carbon than that simulated by the carbon-only TEM, despite climate related increases in carbon uptake. This leads to a larger increase in atmospheric CO_2 concentration and high surface warming. At the same time, consideration of the dependence of carbon uptake on nitrogen availability increases the magnitude of the change in surface temperature required to switch the terrestrial biosphere from being a carbon sink to becoming a carbon source. Thus, the probability of a runaway increase in CO_2 is reduced, but not eliminated.

In our simulations, we assume that the amount of nitrogen in terrestrial ecosystems remains constant, but this nitrogen may be redistributed between vegetation and soil detritus to influence terrestrial carbon storage. Nitrogen inputs from atmospheric nitrogen deposition and nitrogen fixation may also enhance nitrogen availability to potentially alleviate such limitations, but the changes in nitrogen inputs have to be balanced against corresponding changes in nitrogen losses, such as N_2O and N_2 emissions, from terrestrial ecosystems that may result from global change. Hungate *et al.* (2003) estimate that 1.2 to 6.1 Pg N could accumulate in terrestrial ecosystems by the year 2100 from these nitrogen inputs. However, they also show that this nitrogen subsidy is not nearly enough to support the terrestrial uptake of atmospheric CO_2 projected by many models. Future studies should attempt to better account for the influence of nitrogen inputs and losses on terrestrial carbon dynamics.

Our research highlights the importance of including carbon/nitrogen interactions in models used in climate change assessments such as the IPCC. Failure to do so exaggerates the carbon storage capacity of the terrestrial biosphere and underestimates the control needed on CO_2 emissions to stabilize the earth's surface temperature.

Acknowledgments

Authors thank Gian-Kasper Plattner for providing as with the results for Bern model used in Figure 4 and Ron Prinn for comments on the draft of the paper.

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APPENDIX

Changes in terrestrial carbon storage are the result of how carbon fluxes within the land ecosystems and between these ecosystems and the atmosphere (Equations 1-3) vary over time. We examine how CO_2 fertilization and warming influence these fluxes along with the role of carbon/nitrogen interactions to help explain why the temporal patterns of terrestrial carbon storage differ between the carbon-only TEM and the standard TEM.

The influence of CO_2 fertilization alone on these fluxes may be determined by examining the results of the uncoupled simulations in which the climate forcing is fixed. An increase in gross primary productivity in the uncoupled simulation with carbon-only TEM (**Figure A1a**) closely follows the pattern suggested by the increase in the atmospheric CO_2 concentration (Figure 3a). In contrast, the standard TEM simulation indicates that GPP increases more slowly due to nitrogen limitations and eventually becomes constrained by nitrogen availability so that the increase in GPP saturates at a level that is only about 28% of that estimated by the carbon-only TEM simulations during the year 2300 (Figure A1b). Because climate does not change in these simulations, both versions of TEM estimate that autotrophic respiration increases with increasing atmospheric CO_2 concentrations (Figures A1c and A1d) due to the accumulation of vegetation carbon (Figures 5a and 5b). This accumulation occurs because increases in autotrophic respiration and litterfall, which both depend on the amount of vegetation biomass, always lag the increases in GPP caused by increasing atmospheric CO_2 concentrations. As the carbon-only

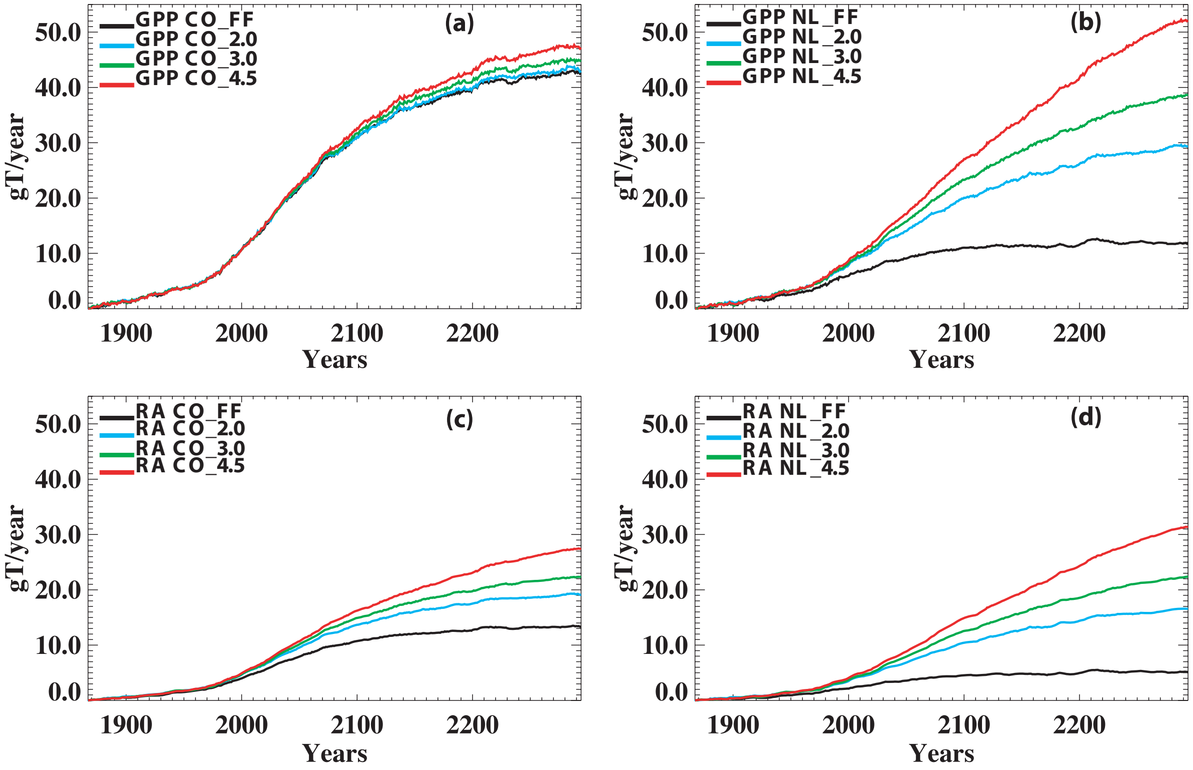

Figure A1. Changes in gross primary production and autotrophic respiration heterotrophic respiration as estimated by the carbon-only TEM **(left column)** and the standard TEM **(right column)**.

TEM estimates much larger GPP inputs to vegetation than the standard TEM, more vegetation biomass accumulates to support rates of autotrophic respiration and litterfall (Figures A2a and A2b) that are almost three and five times higher, respectively, than that estimated by the standard TEM during the year 2300.

Similarly, both versions of TEM estimate that heterotrophic respiration increases with increasing atmospheric CO_2 concentrations (Figures A2c and A2d) due to the accumulation of soil organic carbon (Figures 5c and 5d). This accumulation occurs because increases in heterotrophic respiration, which depends on the amount of soil organic matter, always lags the increases in litterfall caused by increasing atmospheric CO_2 concentrations. As the carbon-only TEM estimates much larger litterfall inputs to the soil detritus pool, more soil organic matter accumulates to support a higher heterotrophic respiration rate than that estimated by the standard TEM. However, as was shown by (McGuire *et al.,* 1997), the specific (per gram C) rate of decomposition also decreases with increasing atmospheric CO_2 concentrations in the standard TEM due to changes in litter quality associated with changes in the vegetation C:N ratio. As a result, an increase in the soil carbon simulated by standard TEM is about 75% of that simulated by carbon-only TEM even though the increase in litterfall estimated by standard TEM is only 20% of that estimated by the carbon-only version. Thus, the differences in the response of terrestrial carbon storage to CO_2 fertilization alone between the two versions of TEM are due to the limitation of primary productivity by nitrogen availability in the standard TEM and changes in tissue chemistry of plants and the resulting detritus.

Terrestrial carbon fluxes also exhibit different sensitivities to climate change between the two versions of TEM. These differences are caused by the influence of climate on nitrogen availability in the standard TEM simulations. While GPP increases with higher temperatures in both TEM versions (Figures 5a and 5b), GPP simulated by the carbon-only TEM shows very little sensitivity to changes in climate whereas GPP shows a much larger sensitivity to the same climate changes in the standard TEM simulations. This enhanced sensitivity is a result of higher temperatures increasing decomposition so that more inorganic nitrogen become available to support higher rates of primary productivity (see below). Autotrophic respiration (R_A) also increases with higher temperatures in both versions of TEM, but R_A is more sensitive to these changes in the standard TEM simulations than the carbon-only simulations. This difference in sensitivity is caused by differences in the accumulation of vegetation carbon, which in turn is determined by the relative sensitivities of GPP and R_A to air temperature between the two TEM versions. In the carbon-only TEM, autotrophic respiration is more sensitive to changes in air temperature than gross primary productivity. As a result, net primary production becomes less with higher temperatures and the vegetation accumulates less carbon under warmer climates than in uncoupled simulation (Figure 5a). In contrast, GPP is more sensitive to air temperature than plant respiration in the standard TEM simulations so that NPP increases with higher air temperatures. The increasing NPP causes vegetation to accumulate additional carbon under warmer climates than in uncoupled simulation (Figure 5b). The differences in the accumulation of vegetation biomass between the two versions of TEM also influence the responses of heterotrophic respiration (R_H) to climate change estimated by the two versions through effects on litterfall. As decomposition rates increase with increasing temperatures, one would normally expect R_H to increase with higher temperatures similar to the response of the standard TEM simulations (**Figure A2d**). However, R_H also depends on the amount of soil detritus available to decompose, which may either increase or decrease based on the relative rates of litterfall inputs to the soil and losses of carbon by decomposition from the soil (Equation 2). In the carbon-only version of TEM, decreases in the accumulation of vegetation biomass with higher temperatures also mean that litterfall will increase more slowly with time (Figure A2a). The slower addition of litterfall carbon to the soil detritus pool along with the more rapid losses of carbon from enhanced decomposition rates cause soil detritus to accumulate much more slowly with warming (Figure 5c). This reduced accumulation of soil detritus with warming has a larger influence on R_H than the direct effect of warming itself in the carbon-only TEM simulations so that heterotrophic respiration decreases with higher temperatures (Figure A2c). In contrast, the increases in the accumulation of vegetation biomass with higher temperatures simulated with the standard TEM also mean that litterfall will increase more rapidly with time (Figure A2b) so that R_H will increase from both the additional amount of carbon available for decomposition and by the enhanced decomposition rates due to warming (Figure A2d). With warming, the losses of soil carbon associated with the enhanced heterotrophic respiration becomes relatively more important than the inputs associated with the enhanced litterfall in the standard TEM simulations so that

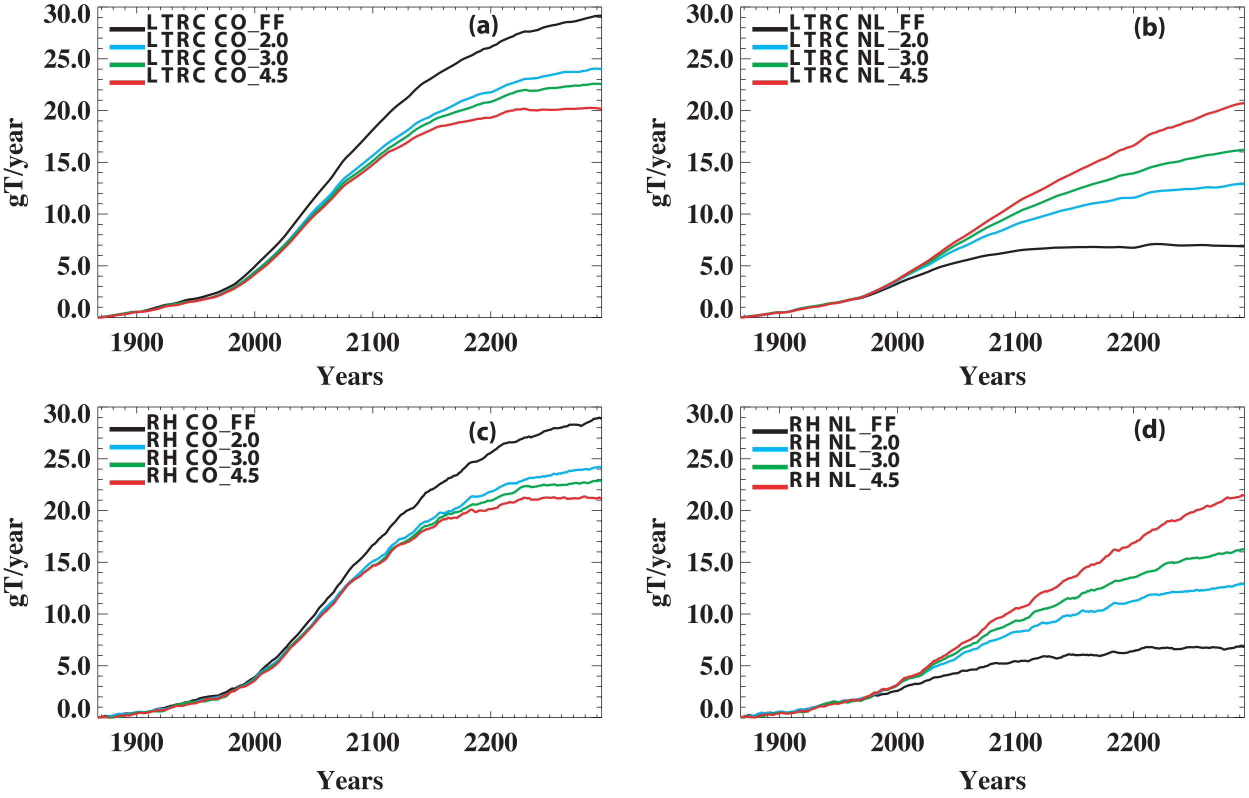

Figure A2. Changes in litterfall carbon and heterotrophic respiration as estimated by the carbon-only TEM **(left column)** and the standard TEM **(right column)**.

soil detritus accumulates more slowly (Figure 5d). Enhanced decomposition with higher temperatures is also a primary mechanism responsible for terrestrial ecosystems switching from being carbon sink to becoming carbon source. When heterotrophic respiration rates become larger than the concurrent litterfall rates, soils lose carbon rather than sequester it. While soils are estimated to be carbon sinks at the beginning of all of the TEM simulations, they become carbon sources during the 22nd century in two simulations with carbon-only TEM (see after year 2150 for S=3.0 K and year 2110 for S=4.5 K) as well as in the simulation with standard TEM for S=4.5 K (see after year 2180). The larger SAT required in the standard TEM for soils to become a carbon source is a result of the influence of litter quality changes, associated with enhanced atmospheric CO_2 concentrations, on specific decomposition rates as described above.

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