

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

ANDREI P. SOKOLOV

Joint Program on the Science and Policy of Global Change, Massachusetts Institute of Technology, Cambridge, Massachusetts

DAVID W. KICKLIGHTER, JERRY M. MELILLO, AND BENJAMIN S. FELZER

The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts

C. ADAM SCHLOSSER

Joint Program on the Science and Policy of Global Change, Massachusetts Institute of Technology, Cambridge, Massachusetts

TIMOTHY W. CRONIN

The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts

(Manuscript received 14 May 2007, in final form 14 November 2007)

ABSTRACT

The impact of carbon–nitrogen dynamics in terrestrial ecosystems on the interaction between the carbon cycle and climate is studied using an earth system model of intermediate complexity, the MIT Integrated Global Systems Model (IGSM). Numerical simulations were carried out with two versions of the IGSM's Terrestrial Ecosystems Model, one with and one without carbon–nitrogen dynamics.

Simulations show that consideration of carbon–nitrogen interactions not only limits the effect of CO₂ fertilization but also changes the sign of the feedback between the climate and terrestrial carbon cycle. In the absence of carbon–nitrogen interactions, surface warming significantly reduces carbon sequestration in both vegetation and soil by increasing respiration and decomposition (a positive feedback). If plant carbon uptake, however, is assumed to be nitrogen limited, an increase in decomposition leads to an increase in nitrogen availability stimulating plant growth. The resulting increase in carbon uptake by vegetation exceeds carbon loss from the soil, leading to enhanced carbon sequestration (a negative feedback). Under very strong surface warming, however, terrestrial ecosystems become a carbon source whether or not carbon–nitrogen interactions are considered.

Overall, for small or moderate increases in surface temperatures, consideration of carbon–nitrogen interactions result in a larger increase in atmospheric CO₂ concentration in the simulations with prescribed carbon emissions. This suggests that models that ignore terrestrial carbon–nitrogen dynamics will underestimate reductions in carbon emissions required to achieve atmospheric CO₂ stabilization at a given level. At the same time, compensation between climate-related changes in the terrestrial and oceanic carbon uptakes significantly reduces uncertainty in projected CO₂ concentration.

1. Introduction

Carbon uptake by terrestrial ecosystems plays an important role in defining changes in the atmospheric CO₂ concentration and changes in climate. In turn, car-

bon 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 CO₂ 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

Corresponding author address: Andrei P. Sokolov, Joint Program on the Science and Policy of Global Change, Massachusetts Institute of Technology, 77 Massachusetts Ave., E40-428, Cambridge, MA 02139-4307.
E-mail: sokolov@mit.edu

terrestrial ecosystem have been the subject of numerous studies carried out in recent years (e.g., Friedlingstein et al. 2006; Matthews 2005; Plattner et al. 2008). However, most of the terrestrial biosphere models currently used in climate change assessments, including the Intergovernmental Panel on Climate Change (IPCC) 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 CO₂ 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 et al. 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. 2008) of earth system models of intermediate complexity (EMICs), the responses of terrestrial carbon dynamics simulated by the Massachusetts Institute of Technology (MIT) Integrated Global System Model version 2 (IGSM2) (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 CO₂ 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 (e.g., Friedlingstein et al. 2006; Matthews 2005; Plattner et al. 2008). 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 likely to be primarily responsible for the responses exhibited by the MIT IGSM2 in that study. In this study, we more directly explore the consequences for the climate system of simulating the terrestrial biosphere with and without carbon–nitrogen interactions. We use the MIT IGSM2 and its biogeochemistry submodel, the Terrestrial Ecosystem Model (TEM) (Melillo et al. 1993; Felzer et al.

2004) with the carbon cycle either coupled to or uncoupled from the nitrogen cycle.

2. Methods

An important feature of TEM is that the model simulates the influence of terrestrial nitrogen dynamics on terrestrial carbon dynamics (Fig. 1). To examine the importance of 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. For this study, we will refer to the standard version of TEM that considers carbon–nitrogen interactions as “CN-TEM” and the version that considers only carbon dynamics as “C-TEM.” A brief description of TEM and the MIT IGSM2 is given in the appendix. Below, we first describe a series of simulations designed to assess the impact of terrestrial carbon–nitrogen interactions on global carbon dynamics. We then describe how we evaluate the sensitivity of terrestrial and oceanic carbon estimated by these simulations to enhanced atmospheric CO₂ concentrations and surface warming.

a. Design of the simulation experiment

To evaluate the impact of carbon–nitrogen interactions on the behavior of terrestrial ecosystems and climate, it is desirable to separate the effects caused by the structural differences between the two versions of TEM from the effects caused by variations in feedbacks between climate and the terrestrial biosphere. Therefore, we carry out several sets of numerical simulations using the two versions of TEM. First, we carry out a set of simulations in which the atmospheric submodel of the IGSM is forced by prescribed changes in atmospheric CO₂ according to the IPCC scenario SP1000 (observed CO₂ concentration until 2004 followed by an increase to stabilization at 1000 ppmv at the year 2350; see Fig. 2a). The absence of feedbacks between terrestrial carbon uptake and atmospheric CO₂ concentration in these simulations allows us to compare the responses of the different versions of TEM to identical changes in atmospheric CO₂ concentrations alone and with changes in climate. This then isolates differences associated with the structural differences between the two versions of TEM.

To evaluate the overall impact of different treatments of carbon–nitrogen interactions on feedbacks among the various earth system components and projections of future climate, we conduct two sets of simulations using the version of the IGSM2 with an inter-

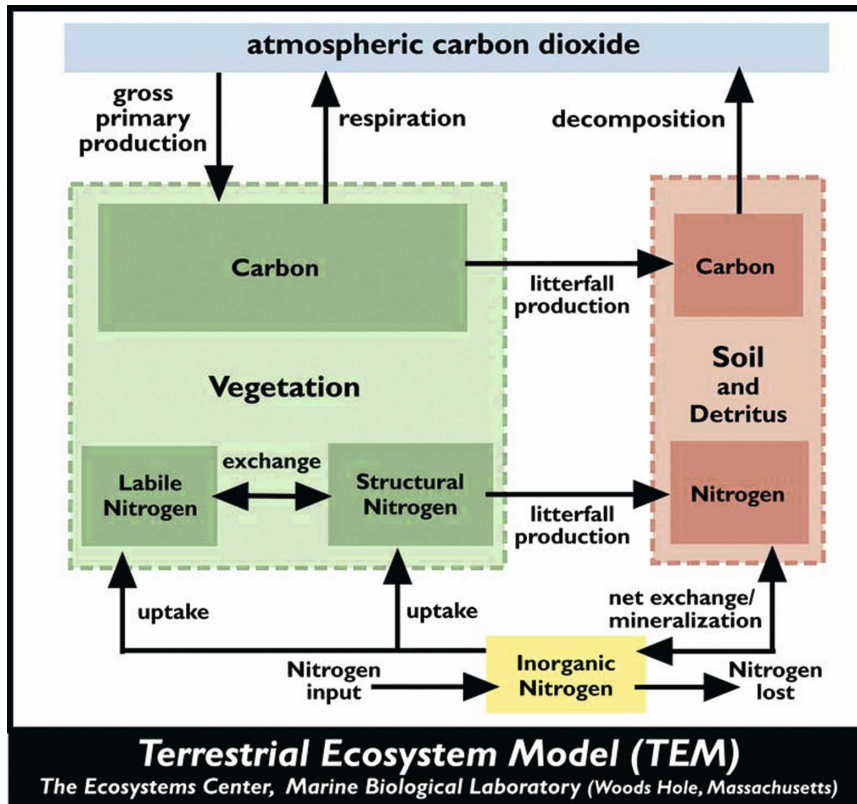


FIG. 1. The Terrestrial Ecosystem Model: State variables are carbon in vegetation, structural nitrogen in vegetation, labile nitrogen in vegetation, organic carbon in soils and detritus, organic nitrogen in soils and detritus, and available soil inorganic nitrogen. Arrows show carbon and nitrogen fluxes: gross primary production, autotrophic respiration, decomposition, litterfall carbon, litterfall nitrogen, N uptake into the structural N pool of the vegetation, N uptake into the labile N pool of the vegetation, the exchange of N between the structural and labile N pools including N resorption from dying tissue into the labile N pool of the vegetation and N mobilized from the labile N pool into the structural N pool of the vegetation, net N mineralization, N inputs from the outside of the ecosystem, and N losses from the ecosystem.

active 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. 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. 2008). Each set contains four simulations (Table 1) with each version of TEM. In the first of the four simulations, changes in CO_2 concentration do not affect climate simulated by the atmospheric submodel. Therefore, TEM is forced by increasing CO_2 with a climate that corresponds to the initial atmospheric CO_2 concentrations. Following the terminology used in previous studies (e.g., Friedlingstein et al. 2003, 2006; Matthews 2005;

Plattner et al. 2008), we refer to this simulation as an “uncoupled simulation.” In three “coupled”¹ simulations, changes in climate are projected using three different values of model sensitivity (S) corresponding to equilibrium surface warming of 2, 3, and 4.5 K in response to the doubling of atmospheric CO_2 concentration (Sokolov and Stone 1998; Sokolov 2006). In all simulations, the IGSM is integrated from year 1861 to 2300.

b. Sensitivity analysis

Different carbon models are often compared in terms of carbon uptake sensitivities to increases in atmo-

¹ In carbon-cycle feedback studies the term “coupled/uncoupled” refers to coupling between the change in CO_2 and climate regardless of whether CO_2 is prescribed (Matthews 2005; Plattner et al. 2008) or simulated by the model (Friedlingstein et al. 2003, 2006).

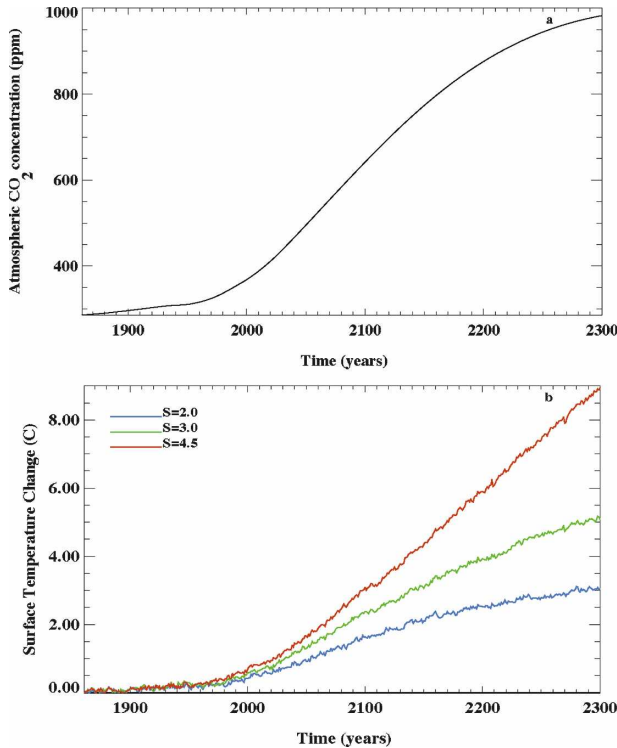


FIG. 2. (a) SP1000 atmospheric CO₂ concentration and (b) changes in surface air temperature in simulations with SP1000 scenario for different values of climate sensitivity using the IGSM.

spheric CO₂ and surface warming (Friedlingstein et al. 2003, 2006; Plattner et al. 2008). In these comparisons, it is assumed that the changes in terrestrial (ΔC_L) and ocean carbon (ΔC_O) can be approximated by linear functions of the changes in CO₂ (ΔCO_2) and surface temperature (ΔT_{srf}). Because the method of calculating these sensitivities is identical for both land and ocean carbon, we present the equations just for the land carbon below:

$$\Delta C_L = \beta_L \Delta \text{CO}_2 + \gamma_L \Delta T_{\text{srf}}, \quad (2.1)$$

where the sensitivity to CO₂ (β_L) can be calculated from the change in terrestrial carbon and CO₂ in the uncoupled simulations, (ΔC_L^{unc}) and ($\Delta \text{CO}_2^{\text{unc}}$), as

$$\beta_L = \Delta C_L^{\text{unc}} / \Delta \text{CO}_2^{\text{unc}}, \quad (2.2)$$

and the sensitivity to surface temperature (γ_L) can be calculated from the change in the carbon and CO₂ in a coupled simulation (ΔC_L^{cou}), as

$$\gamma_L = \{\Delta C_L^{\text{cou}} - \beta_L \Delta \text{CO}_2^{\text{cou}}\} / \Delta T_{\text{srf}}^{\text{cou}}. \quad (2.3)$$

Equation (2.3) is obtained under an assumption that β_L is the same in the coupled and uncoupled simulations. As discussed by Plattner et al. (2008), β_L depends on the CO₂ concentration and may be different between the coupled and uncoupled simulations if atmospheric CO₂ is calculated by the model. Such dependency can be accounted for by calculating β_L for coupled simulations as follows:

$$\beta_L^{\text{cou}} = \{\beta_L + \partial \beta / \partial \text{CO}_2 (\Delta \text{CO}_2^{\text{cou}} - \Delta \text{CO}_2^{\text{unc}})\} \quad (2.4)$$

and then using them in Eq. (2.3) instead of β_L . This, however, requires knowledge of the derivative of β_L with respect to CO₂.

In the simulations with an interactive carbon cycle, the strength of the feedback between climate and the carbon cycle can be expressed in terms of the CO₂ gain (G), that is, the ratio of the increases in CO₂ concentration in the coupled and uncoupled simulations:

$$G = \Delta \text{CO}_2^{\text{cou}} / \Delta \text{CO}_2^{\text{unc}}. \quad (2.5)$$

To evaluate how carbon–nitrogen interactions influence the sensitivity of terrestrial carbon to enhanced atmospheric CO₂ concentrations and surface warming without climate feedbacks, we calculate β_L and γ_L for both the C-TEM and CN-TEM simulations with prescribed atmospheric CO₂. We also examine how CO₂ fertilization assumptions influence these sensitivities.

In TEM, the uptake of atmospheric CO₂ by plants is assumed to follow Michaelis–Menten kinetics, accord-

TABLE 1. Simulations with different versions of TEM. C-TEM simulates only carbon dynamics whereas CN-TEM simulates coupled carbon and nitrogen dynamics.

Simulation	TEM version	Carbon–nitrogen interactions considered?	Climate sensitivity
C_FF	C-TEM	No	Uncoupled simulation with fixed forcing
C_2.0	C-TEM	No	Coupled simulation with $S = 2.0$ K
C_3.0	C-TEM	No	Coupled simulation with $S = 3.0$ K
C_4.5	C-TEM	No	Coupled simulation with $S = 4.5$ K
CN_FF	CN-TEM	Yes	Uncoupled simulation with fixed forcing
CN_2.0	CN-TEM	Yes	Coupled simulation with $S = 2.0$ K
CN_3.0	CN-TEM	Yes	Coupled simulation with $S = 3.0$ K
CN_4.5	CN-TEM	Yes	Coupled simulation with $S = 4.5$ K

ing to which the effect of atmospheric CO_2 at time t on the assimilation of CO_2 by plants is parameterized as follows:

$$f(\text{CO}_2(t)) = (C_{\text{max}} \text{CO}_2(t)) / (kC + \text{CO}_2(t)), \quad (2.6)$$

where C_{max} is the maximum rate of C assimilation, and kC is the CO_2 concentration at which C assimilation proceeds at one-half of its maximum rate (i.e., C_{max}). The sensitivity of plant uptake on kC is defined not by the absolute value of $f(\text{CO}_2(t))$, which decreases with kC , but by the ratio of $f(\text{CO}_2(t))$ to $f(\text{CO}_2(0))$, which increases with kC . This ratio can be approximated as $1 + \alpha \ln(\text{CO}_2(t)/\text{CO}_2(0))$.

The results of CO_2 enrichment studies suggest that plant growth could increase from 24% to 54% in response to doubled CO_2 given adequate nutrients and water (Raich et al. 1991; McGuire et al. 1992; Gundersen and Wullschlegel 1994; Curtis and Wang 1998; Norby et al. 1999, 2005). A 24% response to doubled CO_2 would correspond to a kC value of 215 ppmv CO_2 , whereas a 54% ppmv CO_2 response would correspond to a kC value of 800 ppmv CO_2 . In TEM, a value of 400 ppmv CO_2 is normally chosen for the half-saturation constant kC so that $f(\text{CO}_2(t))$ increases by 37% for a doubling of atmospheric CO_2 from 340 to 680 ppmv CO_2 (McGuire et al. 1992, 1993, 1997; Pan et al. 1998). However, a comparison of the Michaelis–Menten approach to the beta factor approach used by the Bern model (Siegenthaler and Oeschger 1987; Joos et al. 1996) indicates that C-TEM can mimic the CO_2 fertilization response of the Bern model ($\alpha = 0.287$) using a kC value of 150 ppmv CO_2 . Thus, all of the C-TEM and CN-TEM simulations described in section 2a have been conducted using a kC value of 150 ppmv CO_2 . To examine how variations in CO_2 fertilization assumptions might have also influenced the sensitivity of terrestrial carbon to enhanced CO_2 and surface warming, we conducted additional sets of simulations using both C-TEM and CN-TEM with prescribed atmospheric CO_2 concentrations and kC equal to either 400 or 700 ppmv CO_2 . These kC values correspond to kC values of 0.56 and 0.81, respectively.

To evaluate how carbon–nitrogen interactions influence the sensitivity of terrestrial carbon to enhanced atmospheric CO_2 concentrations and surface warming with climate feedbacks, we calculate β_L and γ_L for both the C-TEM and CN-TEM simulations with prescribed CO_2 emissions. We also calculate β_O and γ_O to evaluate the sensitivity of oceanic carbon to enhanced CO_2 and surface warming for these simulations along with G to evaluate the impact of carbon–nitrogen interactions on the strength of the carbon-cycle feedback on climate.

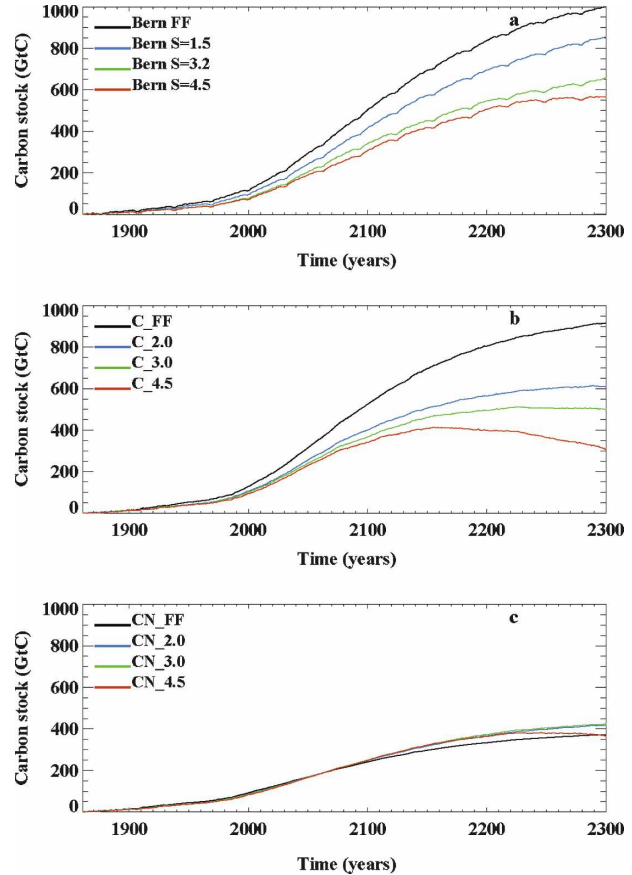


FIG. 3. Changes in the terrestrial carbon simulated by (a) the Bern model, (b) C-TEM, and (c) CN-TEM in the simulations with prescribed changes in atmospheric CO_2 concentration. Note that values of climate sensitivity used in coupled simulations with the Bern model are slightly different from those used in the simulations with the IGSM.

3. Results

a. Influence of carbon–nitrogen interactions on the simulated response of terrestrial ecosystems to CO_2 fertilization and global warming

Changes in terrestrial carbon stocks in the uncoupled simulations with C-TEM (Fig. 3) are very close to changes simulated by the Bern model, which in turn is representative of the behavior exhibited by most earth system models in the Plattner et al. (2008) study. The response of terrestrial carbon stocks to global warming simulated by C-TEM is also similar in pattern, but somewhat larger than the response produced by the Bern model or most other terrestrial carbon models (Friedlingstein et al. 2006; Plattner et al. 2008). The behavior of C-TEM resembles that of the Hadley Centre model (Cox et al. 2000) in that the terrestrial biosphere stops absorbing carbon when surface warming

reaches a threshold. In simulations with C-TEM, this threshold occurs with a 4.5°C increase in global mean surface air temperature (SAT), see Fig. 2b, around year 2150 in the $S = 4.5$ K simulation and around year 2240 in the $S = 3$ K simulation. For other scenarios of CO₂ increase, the corresponding temperature threshold is likely to be different.

In contrast, changes in terrestrial carbon stocks projected by CN-TEM are much lower than those simulated by either the Bern model or C-TEM. In the uncoupled simulation, CN-TEM estimates a gain in terrestrial carbon storage that is only about 40% of the gain projected by the Bern model or C-TEM. In addition, consideration of carbon–nitrogen interactions changes the simulated response of these ecosystems to warming. In the Bern and C-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 CN-TEM simulations, warming causes more carbon to be stored in terrestrial ecosystems, a negative feedback. However, as the SAT continues to increase, a temperature threshold is reached when the feedback switches from negative to positive. Thus, when SAT rises by about 6.5°C around year 2220 in the CN-TEM simulation with $S = 4.5$ K, the terrestrial biosphere becomes a carbon source.

It is worth noting that C-TEM estimates that the terrestrial biosphere accumulates more carbon than CN-TEM with the exception of the simulation with the largest temperature increases. While CN-TEM estimates that carbon storage in the terrestrial biosphere increases by 25%–29% from the year 1861 to 2300, C-TEM estimates that this carbon storage increases by 25%–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 CO₂ and climate are largely the result of the differences in the carbon stored in vegetation. In the C-TEM simulations, vegetation carbon increases by 53%–77% from 1861 to 2300 (Table 2), with the accumulation of vegetation biomass becoming slower with additional warming (Fig. 4a) as a result of enhanced plant respiration. In contrast, the CN-TEM simulations estimate increases of vegetation carbon of only 12%–41% between 1861 and 2300 (Table 2) with biomass accumulation becoming more rapid with additional warming (Fig. 4b) as a result of enhanced nitrogen availability, which supports higher rates of plant productivity. Changes in the soil carbon simulated by the two versions of TEM are qualitatively similar (Figs. 4c,d), but differ in the strength of the response to CO₂ fertilization and warming. In the CN-TEM simulations,

TABLE 2. Changes in the amount of carbon stored in vegetation (VEGC), soils (SOILC), and the terrestrial biosphere (TOTALC) between 1861 and 2300 (expressed as the ratio to corresponding initial value) in the C-TEM (C) and CN-TEM (CN) simulations.

Simulation	VEGC	SOILC	TOTALC
C_FF	1.77	1.71	1.74
C_2.0	1.63	1.32	1.50
C_3.0	1.59	1.15	1.41
C_4.5	1.53	0.87	1.25
CN_FF	1.12	1.40	1.25
CN_2.0	1.25	1.32	1.29
CN_3.0	1.33	1.25	1.29
CN_4.5	1.41	1.06	1.25

carbon storage in soils increases by 6%–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 C-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 climate conditions.

Changes in terrestrial carbon storage are the result of how carbon fluxes within the land ecosystems and between these ecosystems and the atmosphere (see appendix for more details) vary over time. The influence of CO₂ fertilization alone on these fluxes may be determined by examining the results of the uncoupled simulations in which climate forcing is fixed. An increase in gross primary production (GPP) in the uncoupled simulation with C-TEM (Fig. 5a) closely follows the pattern suggested by the increase in the atmospheric CO₂ concentration (Fig. 2a). In contrast, the CN-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 C-TEM simulations during the year 2300 (Fig. 5b). Because climate does not change in these simulations, both versions of TEM estimate that autotrophic respiration increases with increasing atmospheric CO₂ concentrations (Figs. 5c,d) due to the accumulation of vegetation carbon (Figs. 4a,b). This accumulation occurs because increases in autotrophic respiration and litterfall, which both depend on the amount of vegetation biomass, are always smaller than the increases in GPP caused by increasing atmospheric CO₂ concentrations. As the C-TEM estimates much larger GPP inputs to vegetation than the CN-TEM, more vegetation biomass accumulates to support changes in autotrophic respiration (Figs. 5c,d) and litterfall (Figs. 6a,b) that are almost three and five

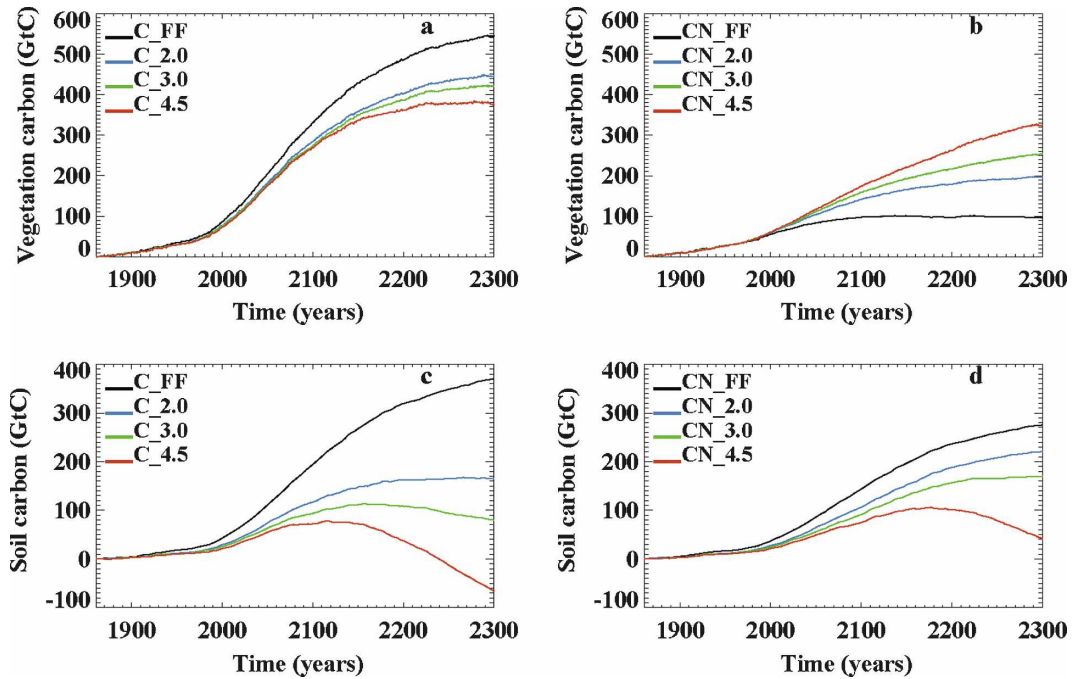


FIG. 4. Changes in (a), (b) the vegetation carbon and (c), (d) soil organic carbon simulated by the (left) C-TEM and (right) CN-TEM in the simulations with prescribed changes in atmospheric CO₂ concentration.

times higher, respectively, than estimated by the CN-TEM during the year 2300.

Similarly, both versions of TEM estimate that heterotrophic respiration increases with increasing atmo-

spheric CO₂ concentrations (Figs. 6c,d) owing to an increase in the soil organic carbon pool (Figs. 4c,d). This accumulation occurs because increases in heterotrophic respiration, which depend on the amount of

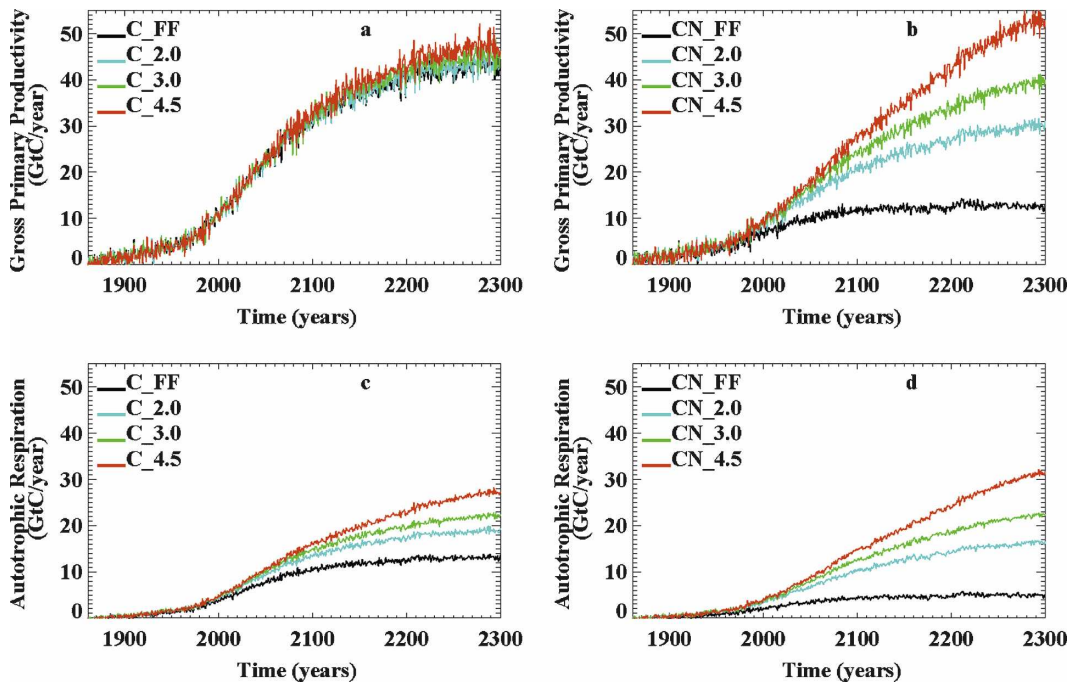


FIG. 5. As in Fig. 4 but for (a), (b) gross primary production and (c), (d) autotrophic respiration.

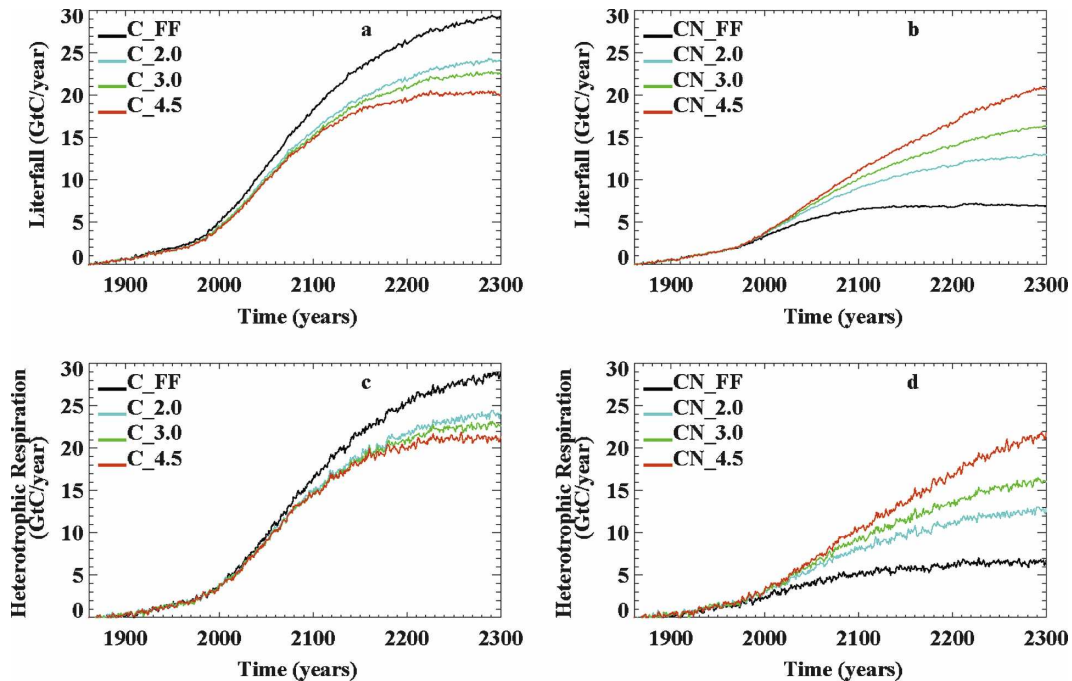


FIG. 6. As in Fig. 4 but for (a), (b) litterfall carbon and (c), (d) heterotrophic respiration.

soil organic matter, are always smaller than the increases in litterfall in the uncoupled simulations. As C-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 CN-TEM. However, as was shown by McGuire et al. (1997), the specific (per gram C) rate of decomposition also decreases with increasing atmospheric CO₂ concentrations in CN-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 CN-TEM is about 75% of that simulated by C-TEM (Figs. 4c,d) even though the increase in litterfall estimated by CN-TEM is only 20% of that estimated by the carbon-only version. Thus, the differences in the response of terrestrial carbon storage to CO₂ fertilization alone between the two versions of TEM are due to the limitation of primary productivity by nitrogen availability in CN-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 CN-TEM simulations. While GPP increases with higher temperatures in both TEM versions (Figs. 5a,b), GPP simulated by C-TEM shows very little sensitivity to changes in climate, whereas GPP shows a much larger sensitivity to the same climate changes in the CN-TEM simulations.

This enhanced sensitivity is a result of higher temperatures increasing decomposition so that more inorganic nitrogen becomes 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 the relative sensitivities of GPP and R_A to air temperature vary between the two TEM versions. This difference in sensitivities leads to the differences in the accumulation of vegetation carbon. In the C-TEM, autotrophic respiration is more sensitive to changes in air temperature than gross primary productivity. As a result, the vegetation accumulates less carbon under warmer climates than in the uncoupled simulation (Fig. 4a). In contrast, GPP is more sensitive to air temperature than plant respiration in the CN-TEM simulations so that vegetation accumulates additional carbon under warmer climates (Fig. 4b).

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 CN-TEM simulations (Fig. 6d). 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 litter-

fall inputs to the soil and losses of carbon by decomposition from the soil. In C-TEM, decreases in the accumulation of vegetation biomass with higher temperatures also mean that litterfall will increase more slowly with time (Fig. 6a). The slower addition of litterfall carbon to the soil detritus pool along with the more rapid losses of carbon from enhanced decomposition rates causes soil detritus to accumulate much more slowly with warming (Fig. 4c). This reduced accumulation of soil detritus with warming has a larger influence on R_H than the direct effect of warming itself in the C-TEM simulations so that heterotrophic respiration decreases with higher temperatures (Fig. 6c). In contrast, the increases in the accumulation of vegetation biomass with higher temperatures simulated with CN-TEM also mean that litterfall will increase more rapidly with time (Fig. 6b) 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 (Fig. 6d). 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 CN-TEM simulations so that soil detritus accumulates more slowly (Fig. 5d).

An increase in decomposition with temperature is also a primary mechanism responsible for terrestrial ecosystems switching from being a carbon sink to becoming a 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 twenty-second century in two simulations with C-TEM (after year 2150 for $S = 3.0$ K and year 2110 for $S = 4.5$ K) as well as in the simulation with CN-TEM for $S = 4.5$ K (after year 2180). The larger SAT required in the CN-TEM for soils to become a carbon source is a result of a climate-related increase in litterfall and changes in specific decomposition rates associated with changes in litter quality described earlier.

In addition to the timing of terrestrial source/sink activities, consideration of carbon–nitrogen interactions has an influence on the location of important terrestrial carbon sinks. For both versions of TEM, terrestrial sinks are projected to occur in boreal, temperate, and tropical regions, but C-TEM estimates larger sinks in the tropics and warmer temperate regions (Fig. 7b), whereas CN-TEM estimates larger sinks in boreal and cooler temperate regions (Fig. 7d). The switch from a sink of atmospheric CO_2 to a source tends to occur

earlier in high-latitude ecosystems where the projected changes in air temperature are larger than at lower latitudes. As GPP is projected to increase across all latitudes throughout the study period by both C-TEM and CN-TEM (Figs. 8a,d), concurrent projected increases in respiration account for the decreases in net carbon uptake of atmospheric CO_2 (Figs. 7a,c) by the terrestrial biosphere. Although net primary production (NPP), which is equal to GPP minus R_A , also generally increases across most latitudes for both versions of TEM (Figs. 8b,e), relatively larger increases in autotrophic respiration cause NPP to decrease at high latitudes under the warmer temperatures occurring toward the end of the $S = 4.5$ K simulations. Increases in GPP and NPP projected by CN-TEM are less than those projected by C-TEM across all latitudes as a result of nitrogen constraints on GPP. While GPP in tropical forests are not currently limited by nitrogen availability in the CN-TEM simulations, the productivity of these forests still depends heavily on net N mineralization rates as the standing stocks of available nitrogen in these ecosystems are small. As net N mineralization rates may not increase rapidly enough with climate change to support the corresponding higher rates of GPP, this GPP becomes more constrained by nitrogen availability as a result of progressive nitrogen limitation (see Luo et al. 2004; Finzi et al. 2006). Increases in heterotrophic respiration projected by C-TEM and CN-TEM (Figs. 8c,f) follow similar patterns as the increases in NPP by the respective models so that terrestrial source/sink activity depends mostly on the small differences between these two carbon fluxes.

b. Influence of carbon–nitrogen interactions on projections of future climate change

Consideration of carbon–nitrogen interactions in terrestrial ecosystems has a large influence on the feedbacks between climate and the carbon cycle. Because both C-TEM and the IGSM ocean carbon model, similar to other ocean carbon models, simulate positive feedbacks with climate, atmospheric CO_2 concentrations are estimated to increase with the increase in surface warming associated with an increase in climate sensitivity (Fig. 9). In contrast, a feedback between climate and the carbon cycle appears to be practically absent in the simulations with the CN-TEM (Fig. 9). 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 CN-TEM. It is worth noting that, in spite of the climate-change-related decrease in terrestrial carbon uptake,

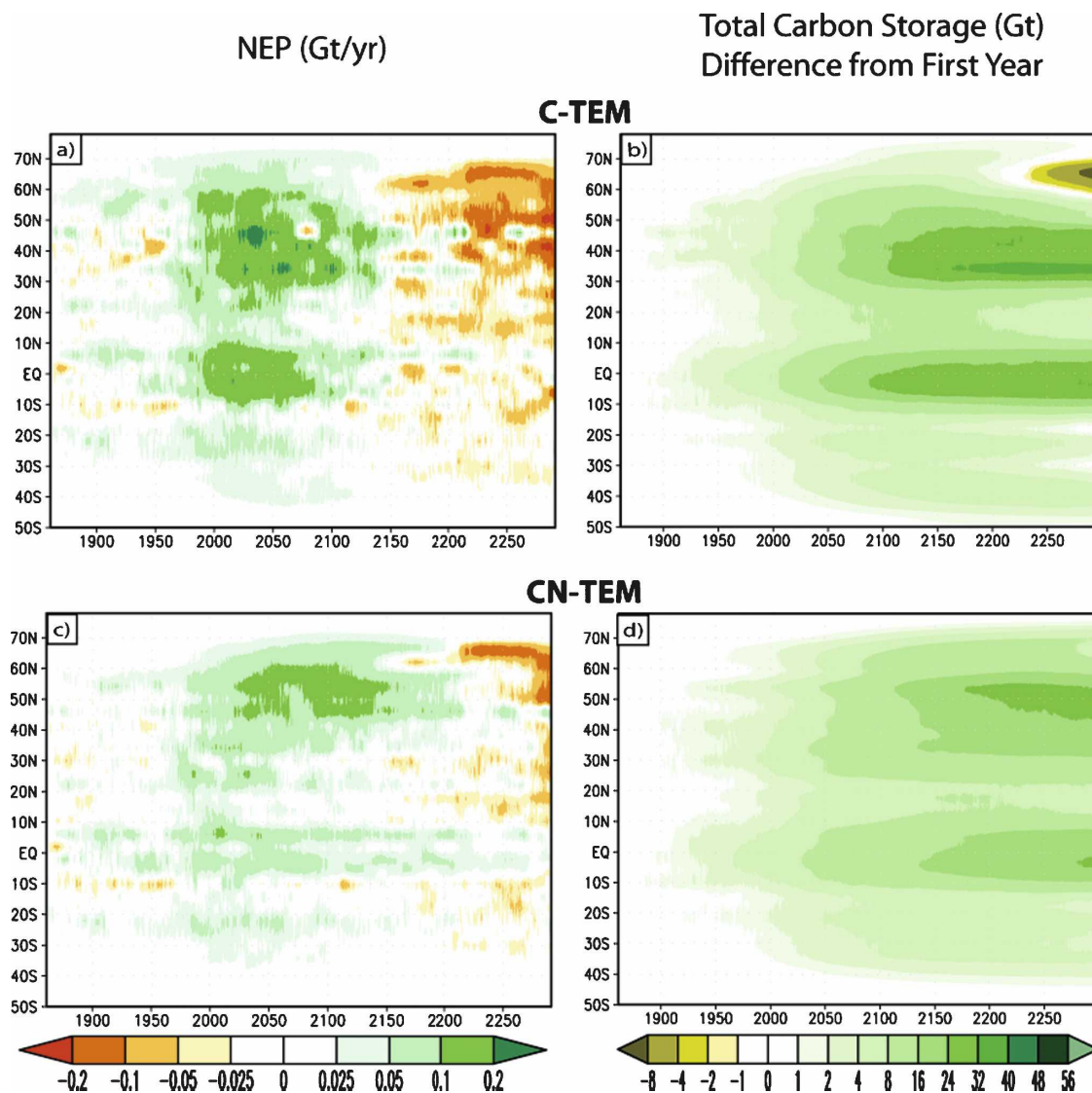


FIG. 7. (a), (c) Latitudinal distribution of the annual net uptake of carbon by terrestrial ecosystems as represented by net ecosystem production (NEP; see appendix) and (b), (d) the accumulation of terrestrial carbon from 1861 to 2300 as simulated by (top) C-TEM and (bottom) CN-TEM for the coupled simulations with climate sensitivity equal to 4.5 K. A positive value of NEP represents a terrestrial sink of CO_2 , whereas a negative value represents a terrestrial source.

the final atmospheric CO_2 concentrations in all of the SP550 simulations (Fig. 9b) and in three out of four SP1000 simulations (Fig. 9a) with the C-TEM are lower than the CN-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 CN-TEM only after year 2240. As a result, SAT increases more in all simulations using the CN-TEM (Fig. 10). The differences in simulated responses between the two TEM versions are more no-

ticeable in the simulations using lower anthropogenic carbon emissions (Figs. 9b and 10b).

c. Influence of carbon–nitrogen interactions on the sensitivity of terrestrial carbon to CO_2 and surface warming

Since changes in the terrestrial carbon can only be roughly approximated by a linear function of changes in CO_2 and SAT [Eq. (2.1)], both β_L and γ_L depend on time period. While all simulations described above have been carried out through year 2300, values of terrestrial and oceanic carbon sensitivity shown in this sec-

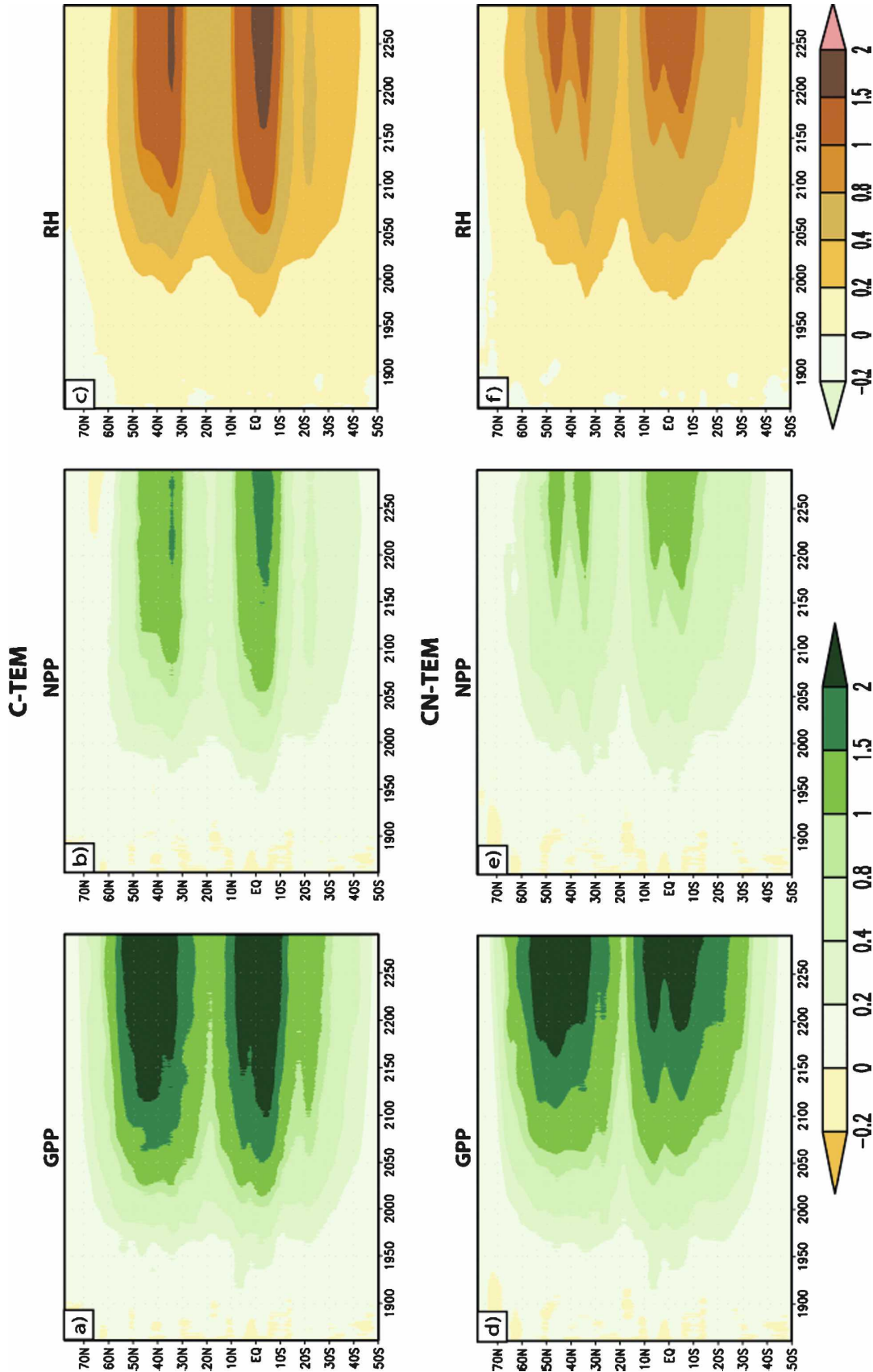


FIG. 8. Changes in the latitudinal distribution of (a), (d) gross primary production; (b), (e) net primary production; and (c), (f) heterotrophic respiration from 1861 to 2300 as simulated by (top) C-TEM and (bottom) CN-TEM for the coupled simulations with climate sensitivity equal to 4.5 K.

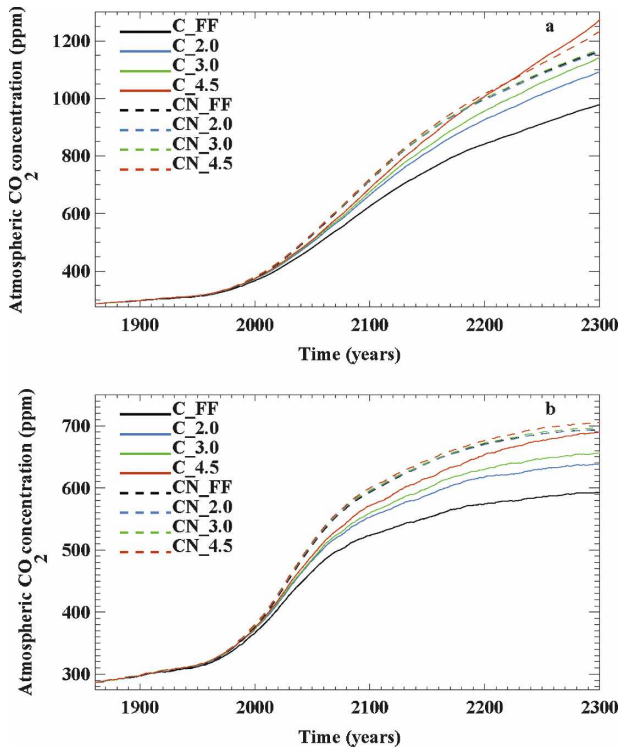


FIG. 9. Atmospheric CO₂ concentrations obtained in simulations with the Bern (a) SP1000 and (b) SP550 emissions scenarios with C-TEM (solid lines) and CN-TEM (dashed lines).

tion are calculated for year 2100, for better comparability with values shown in other studies.

The sensitivity of terrestrial carbon to changes in both CO₂ and climate as simulated by C-TEM with a kC value equal to 150 ppmv CO₂ (Table 3) falls in the ranges of values calculated with other terrestrial models in simulations with prescribed changes in CO₂ concentration (Plattner et al. 2008). As expected, β_L for CN-TEM using a kC value of 150 ppmv CO₂ is a little less than half that for C-TEM as a result of nitrogen limitations on plant productivity. In addition, the CN-TEM results provide positive values of γ_L , indicating enhanced carbon uptake with temperature rather than the negative values as shown by the C-TEM and most other models. As described previously, higher respiration rates associated with higher temperatures reduce net carbon uptake by terrestrial ecosystems in C-TEM, whereas the release of nitrogen during decomposition increases carbon uptake by terrestrial ecosystems in CN-TEM. In other words, the positive sensitivity of carbon to temperature for CN-TEM is a result of an increase in the ability of the terrestrial ecosystem to respond to an increase in CO₂ concentration and can be treated as an increase in β_L .

For both versions of TEM, the sensitivity of terres-

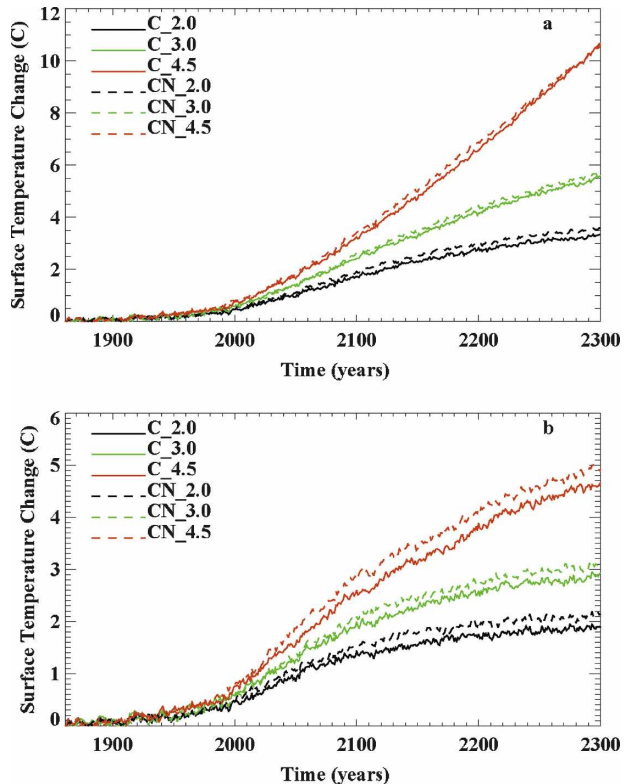


FIG. 10. Changes in surface air temperature in simulations with (a) SP1000 and (b) SP550 emission scenarios with C-TEM (solid lines) and CN-TEM (dashed lines).

trial carbon to surface temperature (measured by the absolute value of γ_L) decreases with the increase of the model climate sensitivity. These changes in sensitivity are explained by changes in the relative responses of GPP and respirations to surface warming (Figs. 5, 6). Similarly carbon sensitivities to temperature change with time. In particular, γ_L for CN-TEM will become negative in the simulation with $S = 4.5$ K (Fig. 3c), as the losses of carbon from respiration and decomposi-

TABLE 3. Terrestrial carbon sensitivities to CO₂ (β_L) and surface warming (γ_L) at different climate sensitivities (2.0, 3.0, or 4.5 K) for C-TEM (C) and CN-TEM (CN) simulations with the Michaelis–Menten half-saturation constant (kC) equal to 150, 400, or 700 ppmv CO₂.

TEM version and kC value	β_L (Gt C ppm ⁻¹)	γ_L (Gt C K ⁻¹)		
		2.0 K	3.0 K	4.5 K
C_150	1.47	-76	-66	-59
C_400	2.71	-86	-75	-67
C_700	3.57	-92	-80	-71
CN_150	0.68	4	4	2
CN_400	0.75	12	11	10
CN_700	0.77	13	12	12

TABLE 4. Sensitivities of terrestrial and ocean carbon to CO₂ (β_L and β_O) and surface warming (γ_L and γ_O) and the corresponding CO₂ gain (G) in the simulations with interactive carbon cycle for climate sensitivity $S = 3$ K using the Bern SP1000 and SP550 emission scenarios.

TEM version and emission scenario	β_L (GtC ppm ⁻¹)	β_O (GtC ppm ⁻¹)	γ_L (GtC K ⁻¹)	γ_O (GtC K ⁻¹)	G
C_SP1000	1.59	1.32	-82	-25	1.15
CN_SP1000	0.67	1.20	4	-10	1.00
C_SP550	1.96	1.66	-78	-24	1.15
CN_SP550	0.83	1.49	5	-13	1.01

tion eventually overwhelm the benefits of enhanced nitrogen availability to GPP.

Simulated responses of the terrestrial biosphere to changes in CO₂ and climate also depend on the assumed value of kC , the Michaelis–Menten half-saturation constant. A change in the value of kC has little impact on the CN-TEM sensitivity to enhanced CO₂ concentrations. Because any increase in GPP in the CN-TEM simulations is restricted by nitrogen availability, the value of β_L only slightly changes with kC . A dependence of β_L on kC becomes even weaker on the longer time scales. In contrast, a change in the value of kC has a large effect on the sensitivity of C-TEM to enhanced CO₂. A change in kC value also changes the sensitivity of net terrestrial carbon uptake to surface warming in both C-TEM and CN-TEM; the absolute value of γ_L increases with the assumed value of kC . In the case of C-TEM, this increase is associated with an increase in vegetation biomass and soil organic carbon due to enhanced GPP. The higher sensitivity of CN-TEM is a result of an increase in the ability of the terrestrial ecosystem to benefit from enhanced nitrogen availability.

An increase in kC also increases the magnitude of surface warming required before the terrestrial biosphere switches from being a carbon sink to becoming a carbon source. In simulations with CN-TEM when kC equals either 400 or 700 ppmv, the terrestrial biosphere starts to be a source of atmospheric CO₂ rather than a sink when SAT rises by more than 11.5° and 13°C, respectively. For C-TEM, the corresponding warming threshold equals 7.5°C when kC is either 400 or 700 ppmv CO₂.

Different treatments of carbon–nitrogen interactions in the simulations with prescribed carbon emissions have a similar effect on terrestrial carbon sensitivity to changes in CO₂ and climate. Sensitivities of both terrestrial and oceanic carbon in the simulations with C-TEM (Table 4) are close to the values obtained in the analogous simulations with other models (Friedlingstein et al. 2006). Values of γ_L and γ_O shown in Table 4, similar to the values presented by Friedlingstein et al.

(2006), are calculated using β_L and β_O , respectively, from the uncoupled simulations. An increase in atmospheric CO₂ concentration in the C-TEM simulation with $S = 3$ K is about 15% larger than in uncoupled simulations (see G in Table 4). In contrast, the atmospheric CO₂ concentrations remain about the same ($G = 1.00$) between the coupled and uncoupled simulations using CN-TEM as described earlier.

Differences between values of β_L and γ_L in the C-TEM simulations with prescribed CO₂ concentration and prescribed carbon emissions are similar to those found in the simulations with the Bern model (Plattner et al. 2008). As discussed by Plattner et al. (2008), the larger sensitivity of terrestrial carbon to temperature in the simulations with an interactive carbon cycle are associated with changes in β_L related to the differences in the atmospheric CO₂ concentrations between the coupled and uncoupled simulations. Since this effect is absent in the simulations with CN-TEM owing to the effects of nitrogen limitations, values of γ_L in simulations with prescribed and projected CO₂ concentration are very similar.

Differences between values of γ_O in simulations with different versions of TEM, for a given emission scenario, are similarly caused by the dependency of β_O on atmospheric CO₂ concentration. Because climate is identical in all uncoupled simulations, derivatives of β_O with respect to CO₂ can be estimated as $\delta \gamma_O / \delta \text{CO}_2$, where δ denotes difference between uncoupled simulations with C-TEM and CN-TEM for each emission scenario. Values of β_O^{cou} [Eq. (2.4)] for C-TEM are equal to 1.25 and 1.58 GtC ppm⁻¹ for the SP1000 and SP550 scenarios, respectively. Corresponding values of γ_O , -12 GtC K⁻¹ for both scenarios, are much closer to the values for CN-TEM than values calculated using β_O from the uncoupled simulations (Table 4).

4. Discussion

Although the importance of carbon–nitrogen interactions on terrestrial carbon sequestration have been described previously (e.g., McGuire et al. 1992, 2001;

Townsend et al. 1996; Den Elzen et al. 1997; Kicklighter et al. 1999; Hungate et al. 2003), it does not appear that most earth system models have yet incorporated the influence of these interactions into their simulations of terrestrial carbon dynamics when assessing the future impacts of global change. The behavior of terrestrial carbon exhibited in the C-TEM simulations is very similar to the behavior exhibited by most earth system models in the Plattner et al. (2008) study. Similar to the findings of the earlier studies, the results of the simulations presented here indicate that consideration of the interactions between the carbon and nitrogen cycles significantly affects the response of the terrestrial biosphere to increases in atmospheric CO₂ concentration and surface air temperature. On one hand, the limitation of carbon uptake by nitrogen availability significantly reduces the effect of CO₂ fertilization in the absence of surface warming. Thus, the estimates of terrestrial carbon sequestration by most earth system models may be overly optimistic. On the other hand, an increase in the surface temperature associated with elevated CO₂ 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 CO₂ 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. Thus, the CN-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, most other earth system models estimate less carbon will be sequestered in the coupled simulations than in the uncoupled simulations. Owing to such differences, the feedbacks between climate and the terrestrial carbon cycle simulated by CN-TEM within the MIT IGSM2 will have different signs than those simulated by most other earth system models.

In addition, consideration of carbon–nitrogen interactions changes the location and timing of important terrestrial carbon sinks and sources. In the CN-TEM simulations, important terrestrial sinks occur in the boreal and cooler temperate ecosystems of the Northern Hemisphere in agreement with inventory and inverse modeling studies (e.g., Schimel et al. 2001; House et al. 2003) although these latter studies also included the effects of land use in their estimates. In contrast, tropi-

cal and warmer temperate ecosystems in the Northern Hemisphere are important terrestrial sinks in the C-TEM simulations. By reducing the sensitivity of terrestrial carbon to elevated CO₂ and surface warming, consideration of carbon–nitrogen interactions requires larger changes in surface warming before terrestrial ecosystems switch from being a sink of atmospheric CO₂ to a source. As a result, terrestrial source activity tends to occur later in simulations of projected climate change and over a more limited area than simulations that do not consider carbon–nitrogen interactions. Thus, the probability of a runaway increase in CO₂ is reduced, but not eliminated. In our simulations, the timing of this switch depends upon CO₂ fertilization assumptions. A larger assumed CO₂ fertilization response (i.e., higher *k_C* values) increases the magnitude of surface warming at which terrestrial ecosystem becomes a source of carbon.

Carbon–nitrogen interactions also affect the influence of the terrestrial biosphere on future atmospheric CO₂ concentrations and the earth's surface temperatures. In most cases, the terrestrial biosphere as simulated by the CN-TEM absorbs less carbon than that simulated by most other earth system models, despite climate-related increases in carbon uptake. This leads to a larger increase in atmospheric CO₂ concentration and high surface warming. As the influence of carbon–nitrogen interactions are more notable in the simulations with lower anthropogenic emissions, accounting for these dynamics is especially important for estimating climate impacts of different economic policies designed to stabilize of the greenhouse gases concentrations in the atmosphere. In addition, the CN-TEM also simulates a negative carbon cycle–climate feedback by the terrestrial biosphere that is at odds with all previous modeling studies on projected climate–carbon cycle interactions (Cox et al. 2000; Friedlingstein et al. 2001, 2003, 2006; Joos et al. 2001; Prentice et al. 2001; Matthews 2005). All of these models simulate a positive carbon cycle–climate feedback similar to the C-TEM results of this study.

While we believe that consideration of carbon–nitrogen interactions in terrestrial ecosystems has improved our understanding of the global carbon cycle, there are a number of issues that still need to be addressed to enhance our ability to realistically simulate global carbon dynamics.

In our simulations, we assume that the amount of nitrogen in terrestrial ecosystems remains constant, but this nitrogen is redistributed between vegetation and soils to influence terrestrial carbon storage. Nitrogen inputs from atmospheric nitrogen deposition (e.g., Townsend et al. 1996; Magnani et al. 2007) and nitrogen

fixation (e.g., Cleveland et al. 1999; Rastetter et al. 2001; Wang et al. 2007) may also enhance nitrogen availability to potentially alleviate such limitations. Townsend et al. (1996) estimate that historical atmospheric nitrogen deposition could account for 25% of the contemporary terrestrial sink, but this effect might diminish in the future as a result of the alleviation of nitrogen limitation or because of the decline of nitrogen-saturated forests in areas of chronically high N deposition (Aber et al. 1998). Magnani et al. (2007) find that net carbon sequestration in temperate and boreal forests are overwhelmingly driven by nitrogen deposition after the effects of forest age and disturbance have been factored out. Hungate et al. (2003) estimate that from 1.2 to 6.1 Pg N could accumulate in terrestrial ecosystems by the year 2100 from nitrogen inputs. However, they also show that this nitrogen subsidy is not nearly enough to support the terrestrial uptake of atmospheric CO₂ projected by many models. The benefits of these nitrogen inputs, however, need to be balanced against nitrogen losses from the ecosystem. These losses include nitrous oxide (N₂O) and dinitrogen (N₂) emissions (e.g., Li et al. 2000; Stange et al. 2000; Kiese et al. 2003) or leaching of nitrate or dissolved organic nitrogen (e.g., Currie and Aber 1997; Cleveland et al. 2004; Harrison et al. 2005) from terrestrial ecosystems. If nitrogen inputs are greater than nitrogen losses, then the response of GPP to increasing atmospheric CO₂ concentrations may be less constrained by nitrogen than indicated by the CN-TEM simulations. Conversely, if nitrogen inputs are less than nitrogen losses, the GPP response to CO₂ may be more constrained than indicated by the CN-TEM simulations. Future studies should attempt to better account for the influence of nitrogen inputs and losses on terrestrial carbon dynamics.

In addition to the short-term effects of environmental factors on terrestrial carbon sequestration, acclimation of vegetation and soil microbial communities may cause the response of terrestrial ecosystems to future climate change to evolve over time. Unlike other models, which may implicitly account for the influence of nitrogen limitation on GPP with approaches such as the use of "biome-specific growth factors" (e.g., Alexandrov et al. 2003), the simulation of nitrogen dynamics in CN-TEM allows the model to account for long-term changes in carbon sequestration associated with changes in nitrogen availability as a result of future climate change.

We have also attempted to account for some of these longer-term effects in the CN-TEM simulations by allowing the C:N ratios of plant tissues and soil detritus to increase with elevated CO₂ (see McGuire et al. 1997).

An unpublished analysis indicates that the changes in the chemistry of plant tissue and detritus as simulated by CN-TEM account for about 50% of the carbon sequestered as a result of CO₂ fertilization. There is, however, an ongoing debate about the degree to which C:N ratios of plant tissues and detritus change with enhanced atmospheric CO₂ concentrations, and the importance of these changes on the ability of terrestrial ecosystems to sequester carbon (e.g., Cotrufo and Ineson 2000; Gifford et al. 2000; Körner 2000; Norby et al. 2001). This uncertainty in the expected changes in the C:N of vegetation tissue and litter has large consequences for developing estimates of future carbon sequestration in terrestrial ecosystems and should be examined further.

Additional sensitivity simulations have indicated that the response of both C-TEM and CN-TEM to climate changes is due primarily to the sensitivity of terrestrial carbon to changes in surface air temperature. Both TEM versions are, on large scales, rather insensitive to changes in precipitation. There are several reasons for this insensitivity. Unlike surface air temperatures, which increase everywhere across the globe, changes in precipitation vary across latitudes with some areas experiencing more precipitation and other areas less. As a result, the effect of changes in precipitation on terrestrial carbon sequestration is rather weak at the global scale. In addition, changes in soil moisture in coupled simulations are quite small, implying that changes in precipitation are, to large degree, offset by changes in evapotranspiration and runoff. It is worth noting that among models used in Plattner et al. (2008) study, only the Loch-Vecode-Ecbilt-Clio-Agism Model (LOVE-CLIM) displays sensitivity of terrestrial carbon to precipitation at the global scale.

Finally, we have not considered the effects of land use change and natural disturbances on terrestrial carbon storage in this study. As these disturbances have a large impact on carbon and nitrogen dynamics of the terrestrial biosphere (e.g., Kasischke et al. 1995, 2005; Harden et al. 2000; McGuire et al. 2001; Houghton 2003; Sitch et al. 2005), consideration of carbon-nitrogen interaction will be even more important.

5. Conclusions

Consideration of carbon-nitrogen interactions has a large impact on the simulation of global carbon dynamics. Nitrogen constraints on plant productivity limit the amount of carbon that can be sequestered by terrestrial vegetation so that atmospheric CO₂ may increase more rapidly in the future, leading to additional warming. Enhanced decomposition associated with surface

warming releases organically bound nitrogen that may alleviate some of these constraints to enhance carbon sequestration, particularly in boreal and temperate ecosystems, with surface warming. This negative feedback from land to climate compensates for the concurrent positive feedback from oceans to reduce the uncertainty in projected CO₂ concentrations into the future. Changes in nitrogen availability to terrestrial vegetation also change the sensitivity of terrestrial carbon to both enhanced atmospheric CO₂ and surface warming over time to influence both the location and timing of terrestrial sinks and sources of atmospheric CO₂.

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 CO₂ emissions to stabilize the earth's surface temperature.

Acknowledgments. The authors thank Gian-Kasper Plattner for providing the results for the Bern model used in Fig. 2 and Ron Prinn for comments on the draft of the paper. This study was supported by grants from the NSF Biocomplexity (ATM-0120468) program; the NASA EOS Interdisciplinary Science (NNG04GH75G) program; the DOE (DOE-DE-FC02-06ER64157); and by funding from MIT Joint Program on the Science and Policy of Global Change, which is supported by a consortium of government, industry, and foundation sponsors.

APPENDIX

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:

- a 2D atmospheric dynamics and physics model
- a mixed layer/anomaly diffusing ocean model (ADOM) with carbon-cycle and sea ice submodels
- a set of coupled land models, the Terrestrial Ecosystem Model (TEM) and the Community Land Model (CLM), that encompass the terrestrial water and energy budgets and terrestrial ecosystem processes

Time steps used in the various submodels range from 10 min for atmospheric dynamics to 1 month for TEM,

reflecting differences in the characteristic time scales of the various processes simulated by the IGSM.

a. Atmospheric dynamics and physics

The MIT two-dimensional 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, 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 4° resolution in latitude and 11 levels in the vertical dimension.

The MIT 2D atmospheric dynamics and physics model allows up to four 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, and 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), which was shown to be the main source of differences in climate sensitivity of different GCMs (e.g., Cess et al. 1990; Colman 2003).

b. Ocean component

The ocean component of the IGSM2.2 consists of a model of an upper-ocean layer with horizontal resolution of 4° in latitude and 5° in longitude and a 3000-m-deep anomaly diffusing ocean model (ADOM) beneath (Sokolov et al. 2007). The upper-ocean layer is divided into two sublayers 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). The mixed layer model also includes a specified vertically integrated horizontal heat transport by the deep oceans, a so-called Q flux. In contrast with conventional upwelling–diffusion models, diffusion in ADOM is not applied to temperature itself but to the temperature difference from its values in a present-day climate simulation. The

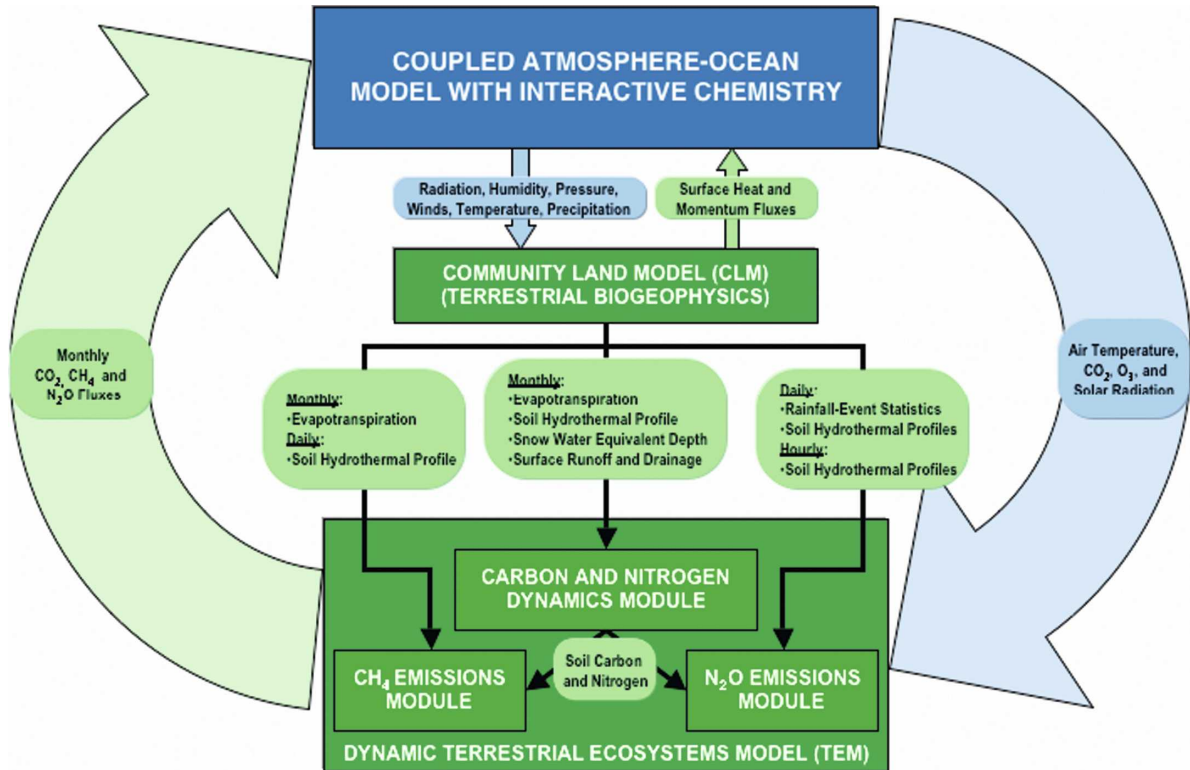


FIG. A1. Global Land System framework.

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 2D ocean carbon model used in the current version of the IGSM2.2, in spite of its simplicity, reproduces well changes in the carbon uptake simulated by the 3D ocean model used in the IGSM2.3 (see Sokolov et al. 2007 for details). As discussed in section 3c, it has sensitivity to changes in both CO₂ and climate that are similar to the sensitivities of other ocean carbon models.

c. Land and vegetation processes

Within the IGSM2.2, land processes are represented with a Global Land System (GLS) framework (Fig. A1) in which water and energy dynamics are simulated by CLM version 2 (Bonan et al. 2002; Zeng et al. 2002) and terrestrial carbon and nitrogen dynamics are simulated by 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 (Fig. 1), 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 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 and standing dead and soil organic matter). In TEM, the carbon in vegetation biomass and detritus are each represented by a single pool (Fig. 1). 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:

$$\Delta\text{VEGC} = \text{GPP} - R_A - L_C, \quad (\text{A.1a})$$

$$\Delta\text{VEGC} = \text{NPP} - L_C, \quad (\text{A.1b})$$

$$\Delta\text{SOILC} = L_C - R_H, \quad (\text{A.2})$$

$$\Delta\text{TOTALC} = \Delta\text{VEGC} + \Delta\text{SOILC}, \quad (\text{A.3a})$$

$$\Delta\text{TOTALC} = \text{NPP} - R_H = \text{GPP} - R_A - R_H. \quad (\text{A.3b})$$

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 [Eq. (A.3a)] or by the difference between NPP and R_H [Eq. (A.3b)], which is also known as net ecosystem production (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 effect of nitrogen limitation on GPP is determined by first calculating GPP_C assuming no nitrogen limitation:

$$\text{GPP}_C = f(\text{CO}_2)f(\text{PAR})f(\text{CANOPY})f(\text{LEAF})f(T)f(\text{O}_3), \quad (\text{A.4})$$

where CO_2 is atmospheric CO_2 concentration, PAR is photosynthetically active radiation, CANOPY is the relative state of a vegetation canopy recovering from disturbance as compared to the canopy state of a mature stand, LEAF is the monthly leaf area relative to the maximum leaf area of a stand, T is air temperature, and O_3 is atmospheric ozone concentration. Details of Eq. (A.4) have been described elsewhere (e.g., Raich et al. 1991; McGuire et al. 1992, 1995, 1997; Pan et al. 1998; Tian et al. 1999; Felzer et al. 2004).

GPP_N is then calculated based on the effects of nitrogen supply on net primary production (NPP_N):

$$\text{NPP}_N = P_{\text{CN}}(\text{NUPTAKE} + \text{NMOBIL}), \quad (\text{A.5a})$$

$$\text{GPP}_N = \text{NPP}_N + R_A, \quad (\text{A.5b})$$

where P_{CN} is the carbon to nitrogen ratio (C:N) of newly produced plant tissue, NUPTAKE is the amount of inorganic nitrogen acquired by plants from the soil, and NMOBIL is the amount of vegetation labile nitrogen mobilized during a particular month (McGuire et al. 1997; Pan et al. 1998; Tian et al. 1999). Monthly GPP is then determined as follows:

$$\text{GPP} = \min(\text{GPP}_C, \text{GPP}_N). \quad (\text{A.6})$$

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 doubling of atmospheric CO_2 from 340 to 680 ppmv (McGuire et al. 1997). Thus, vegetation biomass will contain more carbon per gram nitrogen under enhanced atmospheric CO_2 concentrations with similar climate conditions in our simulations.

Another feature of carbon–nitrogen interactions in TEM is that the model also simulates the release of inorganic nitrogen from soil organic matter (i.e., mineralization) during decomposition. While no nitrogen is assumed to be added or lost from terrestrial ecosystems, TEM accounts for the influence of immobilization of nitrogen by soil microbes when determining how much recycled nitrogen may be available for uptake by plants (Raich et al. 1991). Contrary to the assumptions reported by Houghton et al. (1998), most of the nitrogen mineralized from soil organic matter, about 70% on average, is retained in the soil due to immobilization in our model simulations. The rest of the nitrogen is then added to the inorganic nitrogen pool where it is available for uptake by plants to support plant productivity. Net N mineralization, however, varies across the globe so that higher-latitude ecosystems generally have less recycled nitrogen available for plant uptake than tropical ecosystems (McGuire et al. 1992). 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 owing 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).

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). The prescribed distribution of land cover does not change during the simulation. Thus, land surface attributes that depend on land cover—such as albedo, roughness, and field capacity—also do not change during our simulations. 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 of precipitation across a 4° latitudinal band. As a result, the IGSM2.2 simulates the present-day seasonal cycle of land precipitation, evapotranspiration, soil moisture, and terrestrial carbon fluxes rather well (Schlosser et al. 2007). However, the IGSM2 does not simulate any changes in longitudinal variability that may occur with climate change. In spite of this shortcoming, comparisons of the TEM response to climate changes simulated by the 2D IGSM and two different 3D AGCMs [GISS and Geophysical Fluid Dynamics Laboratory (GFDL)] found very good agreement in large-scale changes of NPP as well as soil and vegetation carbon (Xiao et al. 1997).

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 not included in the analyses presented in this paper.

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