

Influence of carbon-nitrogen cycle coupling on land model response to CO₂ fertilization and climate variability

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Received 24 October 2006; revised 27 June 2007; accepted 23 August 2007; published 14 December 2007.

[1] Nutrient cycling affects carbon uptake by the terrestrial biosphere and imposes controls on carbon cycle response to variation in temperature and precipitation, but nutrient cycling is ignored in most global coupled models of the carbon cycle and climate system. We demonstrate here that the inclusion of nutrient cycle dynamics, specifically the close coupling between carbon and nitrogen cycles, in a terrestrial biogeochemistry component of a global coupled climate system model leads to fundamentally altered behavior for several of the most critical feedback mechanisms operating between the land biosphere and the global climate system. Carbon-nitrogen cycle coupling reduces the simulated global terrestrial carbon uptake response to increasing atmospheric CO₂ concentration by 74%, relative to a carbon-only counterpart model. Global integrated responses of net land carbon exchange to variation in temperature and precipitation are significantly damped by carbon-nitrogen cycle coupling. The carbon cycle responses to temperature and precipitation variation are reduced in magnitude as atmospheric CO₂ concentration rises for the coupled carbon-nitrogen model, but increase in magnitude for the carbon-only counterpart. Our results suggest that previous carbon-only treatments of climate-carbon cycle coupling likely overestimate the terrestrial biosphere's capacity to ameliorate atmospheric CO₂ increases through direct fertilization. The next generation of coupled climate-biogeochemistry model projections for future atmospheric CO₂ concentration and climate change should include explicit, prognostic treatment of terrestrial carbon-nitrogen cycle coupling.

Citation: Thornton, P. E., J.-F. Lamarque, N. A. Rosenbloom, and N. M. Mahowald (2007), Influence of carbon-nitrogen cycle coupling on land model response to CO₂ fertilization and climate variability, *Global Biogeochem. Cycles*, 21, GB4018, doi:10.1029/2006GB002868.

1. Introduction

[2] The response of land ecosystems to increasing atmospheric CO₂ concentration is an important control on the fraction of fossil fuel emissions of CO₂ that remains in the atmosphere [Tans *et al.*, 1990]. This control is modulated by the response of land ecosystems to climate variability and climate changes [Bousquet *et al.*, 2000; Ciais *et al.*, 2005; Goulden *et al.*, 1996] induced in part by the atmospheric accumulation of CO₂ [Friedlingstein *et al.*, 2006]. Interactions between carbon and nitrogen cycles within land ecosystems play an important role in determining the long-term evolution of plant, litter, and soil organic matter pools of carbon and nitrogen [Chapin *et al.*, 1986; Vitousek and Howarth, 1991], as well as the response of these pools to changes in atmospheric composition and climate [Field *et al.*, 1992]. Modeling studies have noted that these interactions are likely to influence the future trajectories of atmospheric CO₂ concentration and associated climate

changes [Holland *et al.*, 1997; McGuire *et al.*, 1992, 2001; Moorhead *et al.*, 1986; Rastetter *et al.*, 1997, 1991], but to date no coupled climate-carbon cycle modeling studies have included an explicit treatment of the terrestrial nitrogen cycle [Friedlingstein *et al.*, 2006].

[3] Hungate *et al.* [2003] showed that the responses of several current land ecosystem models to increasing CO₂ concentration over the next century are stoichiometrically inconsistent with independent estimates of mineral nitrogen supply. Their analysis suggests that treating the nitrogen cycle explicitly in such models would lead to reduced land ecosystem sensitivity to changes in atmospheric CO₂. Enhanced growth due to increasing CO₂ increases plant demand for mineral nitrogen, while fresh litter inputs associated with increased growth can increase microbial demand for mineral nitrogen through enhanced immobilization potential. These effects could increase nitrogen limitation under conditions of increasing CO₂, producing a decline over time in the strength of the negative feedback between land ecosystems and atmospheric CO₂ [Luo *et al.*, 2004; Miller, 1986; Reich *et al.*, 2006].

[4] A recent intercomparison of coupled climate-carbon cycle models demonstrates a range of responsiveness of

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modeled land ecosystems to increasing temperature and increasing atmospheric CO₂ [Friedlingstein et al., 2006]. For all models the land ecosystem response to temperature is a positive feedback, with warmer temperatures producing an increase in atmospheric CO₂. Both net primary production (NPP) and heterotrophic respiration (HR) are enhanced by warming in these models, but the temperature effect on HR is stronger, resulting in a positive feedback. By excluding a prognostic nitrogen cycle and carbon-nitrogen (C-N) cycle coupling, this current generation of models misses a potentially important feedback connecting HR and NPP, whereby the supply of mineral nitrogen necessary to support new plant growth in nonagricultural systems comes mainly from nitrogen mineralization accompanying the decay of older soil organic matter [Bonan, 1990; Field et al., 1992; Pastor and Post, 1988; Schimel et al., 1990; Vitousek and Howarth, 1991]. NPP and HR are both sensitive to soil moisture status, and so we also expect that introducing realistic C-N feedbacks within the terrestrial ecosystem will alter the model responses to variation in precipitation [Betts, 2005; Prior et al., 1997; Santiago et al., 2005; Wahren et al., 2005].

[5] Here we test two major hypotheses: first, that introducing a prognostic nitrogen cycle and C-N coupling into a global land surface process model significantly reduces the strength of the terrestrial CO₂ fertilization effect; and second, that C-N coupling results in a positive feedback between HR and NPP which reduces the strength of the net land carbon cycle response to changes in temperature. Both of these hypotheses are stated relative to a model which does not include a prognostic nitrogen cycle or C-N coupling. In terms of the signs and strengths of major feedbacks between the terrestrial biosphere and the global climate system, we expect that introducing C-N coupling reduces the strength of the negative carbon cycle feedback from CO₂ fertilization of land ecosystems, leading to larger atmospheric accumulations of fossil fuel-derived CO₂ than predicted by carbon-only models. We also expect a global reduction in the sensitivity of net land carbon exchange to temperature change, leading to a smaller net land carbon source to the atmosphere due to warming.

[6] Our study uses a recently developed model of coupled terrestrial carbon, nitrogen, water, and energy dynamics [Thornton and Zimmermann, 2007], implemented as a component of the Community Climate System Model (CCSM) [Collins et al., 2006]. The model includes the capability to run with and without a fully prognostic nitrogen cycle. We use that capability to evaluate the influence of terrestrial carbon-nitrogen cycle coupling on the response of the terrestrial biosphere to increasing atmospheric CO₂ concentration, increasing mineral N deposition, and variability in temperature and precipitation. Simulations here are forced with multiyear output from the atmospheric model component of CCSM in an offline mode. Results documenting the influence of terrestrial C-N coupling in the fully coupled CCSM will be reported separately.

2. Methods

2.1. Model Description

[7] The land biogeochemistry model used here is the result of merging the biophysical framework of the Com-

munity Land Model (CLM 3.0) [Bonan and Levis, 2006; Dickinson et al., 2006; Oleson et al., 2004] with the fully prognostic carbon and nitrogen dynamics of the terrestrial biogeochemistry model Biome-BGC (version 4.1.2) [Thornton et al., 2002; Thornton and Rosenbloom, 2005]. The resulting model, CLM-CN (Community Land Model with prognostic Carbon and Nitrogen) is fully prognostic with respect to all carbon and nitrogen state variables in the vegetation, litter, and soil organic matter, and retains all prognostic quantities for water and energy in the vegetation-snow-soil column from CLM 3.0. Detailed descriptions for all biogeochemical components of CLM-CN, and for those aspects of the biophysical framework modified to accommodate prognostic vegetation structure, are provided as an electronic supplement (see Text S1).¹

2.2. Simulation Protocol

[8] Our objective here is to examine the effects of introducing coupled C-N dynamics in the land component of a coupled climate system model. Our approach is to perform a series of offline simulations in advance of the much more computationally demanding fully coupled carbon-(nitrogen)-climate experiments. By “offline” we mean a simulation in which the land model component of the coupled system is forced by a prescribed data set of atmospheric fluxes and states. For these simulations we created such a data set by extracting 25 years (a) of hourly results from the atmospheric model component of CCSM (the Community Atmosphere Model, CAM [Collins et al., 2006]), from an experiment in which CAM and CLM were run in a partially coupled mode (prescribed sea surface temperatures and sea ice distributions). The coupling frequency between CLM and CAM in the coupled system is 1 h, so this sampling strategy does not represent any additional aggregation of atmospheric states or fluxes.

[9] Our goal here was to obtain a sample of CAM output that would be similar in mean state and variability to the climate simulated by the fully coupled model [cf. Doney et al., 2006], such that our analysis provides a preliminary indication of the dynamics of the fully coupled system. Preliminary evaluation of carbon cycle predictions from CLM-CN when forced with reanalysis surface weather fields showed reasonable results for predicted net primary production in most vegetation types, with underpredictions in the coldest regions (arctic tundra and larch forest) [Thornton and Zimmermann, 2007].

[10] The model includes carbon and nitrogen pools with long turnover times, and the long-term accumulation of mass in these slow pools depends in part on a balance between inputs and outputs of nitrogen that are very small relative to the rates of internal nitrogen cycling [Chapin et al., 1986; Vitousek and Howarth, 1991]. The model spin-up strategy described by Thornton and Rosenbloom [2005] (accelerated decomposition method) was used to bring the carbon and nitrogen states into dynamic equilibrium with respect to the 25-a sample of CAM output. Spin-up required about 750 model years, achieved by cycling the 25-a time series of atmospheric forcing. During spin-up, atmospheric

¹Auxiliary materials are available in the HTML. doi:10.1029/2006GB002868.

Table 1. Summary of Experiments^a

Experiment	CO ₂ Forcing	N _{dep} Forcing ^b	V _{cmax} Scaling ^c
CN	ca. 1850	ca. 1850	1.0
CN+co2	transient	ca. 1850	1.0
CN+ndep	ca. 1850	transient	1.0
CN+co2ndep	transient	transient	1.0
C	ca. 1850	–	1.0
C+co2	transient	–	1.0
C _r	ca. 1850	–	0.68
C _r +co2	transient	–	0.68

^aAll experiments are 251 years (a) duration (1850–2100).

^bNitrogen deposition forcing (not relevant for experiments C and C_r).

^cMultiplier applied to V_{cmax} (via fraction of leaf nitrogen in Rubisco enzyme) for all plant functional types.

CO₂ was kept constant at 283.6 parts per million by volume (ppmv), its assumed value at 1850 A.D. Land cover was assumed constant during spin-up and throughout the experiments, using the values circa 1850 A.D. from *Feddema et al.* [2005].

[11] The nitrogen deposition fields used in this study were generated by the three-dimensional chemistry transport MOZART-2 (Model for Ozone and Related Tracers, version 2 [Horowitz *et al.*, 2003]). In all simulations (preindustrial, present-day and future), MOZART uses meteorological data sets valid for the period of interest, on the basis of simulations by the Parallel Climate Model [Washington *et al.*, 2000]. The MOZART-2 simulations were performed at the horizontal resolution of 2.8°. All the dynamical and chemical processes simulated by MOZART-2 are performed with a model time step of 20 min, while the nitrogen deposition fluxes are archived monthly. For additional information on the present-day and future simulations, the reader is referred to *Lamarque et al.* [2005]. The preindustrial simulation is similar to the present-day simulations, except that all emissions associated with anthropogenic activities (excluding biomass burning) are explicitly set to 0. Nitrogen deposition from the MOZART-2 preindustrial simulation was used for the CLM-CN spin-up simulation.

[12] To allow direct evaluation of the effects of C-N coupling, the spin-up was performed with the regular nitrogen cycle behavior in effect and also in carbon-only mode. Switching from the carbon-nitrogen to the carbon-only model configuration results in a more productive model mean state, characterized by increased vegetation productivity and larger steady state carbon accumulations in vegetation, litter, and soil organic matter. To help distinguish the effects of increased model mean state in the absence of C-N coupling from the direct effects of nitrogen limitation, carbon-only experiments were repeated with a 32% reduction in maximum carboxylation rate (V_{cmax}) (Table 1). The magnitude of this scaling factor was based on comparison of gross primary production from initial carbon-only simulation (about 177 PgC a⁻¹, preindustrial) with the estimate from the third IPCC assessment (120 PgC a⁻¹) [Houghton *et al.*, 2001]. A similar scaling strategy was used by *McGuire et al.* [1992] in their evaluation of how C-N interactions influence modeled net primary production.

[13] Multiple off-line experiments of duration 251 a (nominally 1850–2100 A.D.) were initiated from the spun-up states (Table 1). Control experiments were per-

formed from each spin-up with constant CO₂ and nitrogen deposition. Experiments with increasing atmospheric CO₂ used the historical record through year 2000, and followed the SRES A2 concentration scenario for years 2000–2100 [Nakicenovic and Swart, 2000]. Experiments with increasing nitrogen deposition used a linear interpolation between MOZART-2 outputs for years 1890, 2000, 2050, and 2100.

2.3. Analyses

[14] Following *Friedlingstein et al.* [2003], we express the sensitivity of the land carbon cycle to increasing atmospheric CO₂ (β_L) as:

$$\beta_L = \frac{\Delta C_L}{\Delta C_A}, \quad (1)$$

where ΔC_L is the change in global total land carbon stock (PgC) over a given time period and ΔC_A is the change in atmospheric CO₂ concentration (ppmv) over the same period. Because our experiments are performed in offline as opposed to coupled mode and lack a radiatively driven climate change signal, we cannot calculate a temperature sensitivity parameter directly analogous to γ_L from *Friedlingstein et al.* [2003]. Instead, we estimate the sensitivities of the land carbon cycle to interannual variations in temperature (S_T) and precipitation (S_P) as the multiple least squares regression slopes for net ecosystem exchange of carbon (NEE) versus annual mean temperature and annual mean precipitation.

2.4. Model Archive

[15] Exact source code and routines for analysis of model output used in this study are archived at the Oak Ridge National Laboratory Distributed Active Archive Center, in the Biogeochemistry Model Archive (http://www.daac.ornl.gov/model_intro.shtml), following the model archiving guidelines provided by *Thornton et al.* [2005].

3. Results

3.1. Steady State Stocks and Fluxes

[16] Introduction of C-N coupling has a significant effect on the prognostic model carbon stocks at steady state (Figure 1 and Table 2). N limitation reduces total carbon stock by 43% compared to the carbon-only model in the control experiments. The reduction is greater for soil organic matter (55%) than for vegetation carbon (36%), with intermediate reductions for litter and coarse woody debris pools. N limitation also has a significant effect on the modeled carbon fluxes at steady state (Figure 1 and Table 3). Gross primary production (GPP) is reduced by 43% in control experiments, with a smaller reduction in autotrophic respiration (39%) and a larger reduction in heterotrophic respiration (47%), and a substantially larger reduction in C losses due to fire (54%). Under the carbon-only model many regions with moderate to high net primary production are maintained at relatively low total vegetation carbon by large mean annual fire fluxes. Under the C-N model nitrogen loss from fire in these same regions constrains productivity and reduces steady state fire fluxes

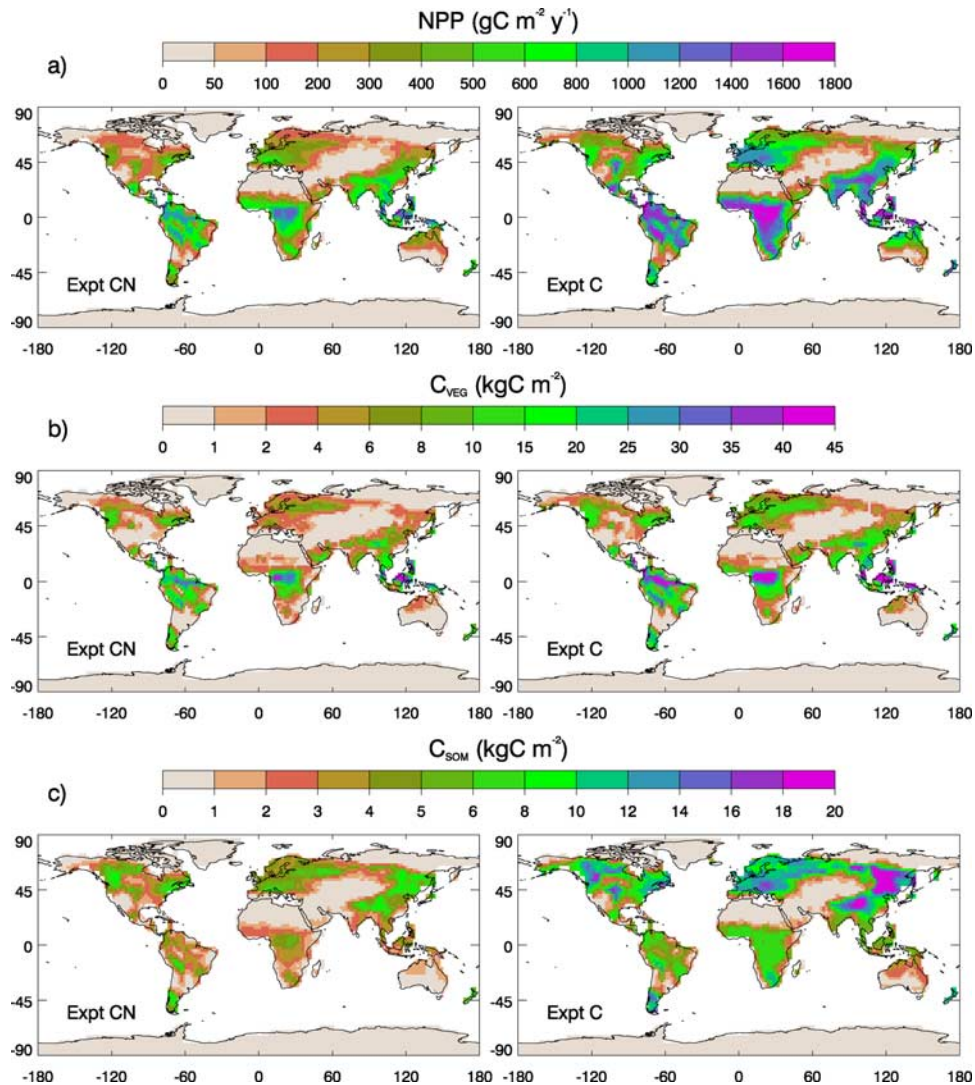


Figure 1. Example annual mean flux and state variables from final 25 a of control simulations for C-N (Experiment CN) and carbon-only (Experiment C) model configurations. (a) Net primary production (NPP). (b) Total vegetation carbon (C_{veg}). (c) Total soil organic matter carbon (C_{SOM}).

(Table 3, fire amounts for experiment C relative to experiment CN).

3.2. Response to Increasing CO_2 and Nitrogen Deposition

[17] Introduction of C-N coupling significantly reduces the carbon uptake response to increasing atmospheric CO_2 concentration (Tables 2 and 4). Total carbon uptake due to increasing atmospheric CO_2 concentration over the historical period (years 1850–2000) was 3.7 times higher for the carbon-only model than for the C-N model (Table 4), with mean uptake over the period 1981–2000 of 3.8 ± 0.4 and $1.1 \pm 0.1 \text{ PgC a}^{-1}$ for experiments C + co_2 and CN + co_2 , respectively. These differences persist under the assumed future CO_2 trajectory: total uptake is 3.8 times higher for carbon-only than for C-N model over the period 2000–2100 AD, with mean uptake over the period 2081–2100 of

10.8 ± 0.5 and $2.8 \pm 0.2 \text{ PgC a}^{-1}$ for experiments C + co_2 and CN + co_2 , respectively (Table 4). Anthropogenic N deposition by itself produces a mean uptake of 0.24 ± 0.03 and $0.73 \pm 0.09 \text{ PgC a}^{-1}$ for the periods 1981–2000 and 2081–2100, respectively (experiment CN + ndep , Table 4). The interaction effect of increasing CO_2 and increasing N deposition on total land carbon uptake is +2.5% for the period 1850–2000, but increases to +11.3% for the period 2000–2100 (experiment CN + co_2ndep , Table 4), suggesting an increase in N limitation under rising CO_2 .

[18] Introduction of C-N coupling shifts the partitioning of carbon accumulated due to CO_2 fertilization away from soil organic matter and toward vegetation pools. Of the total carbon uptake under increasing CO_2 , the fraction entering soil organic matter is 50–58% lower and the fraction entering vegetation is 18–22% higher for experiment CN + co_2 compared to experiment C + co_2 (Table 4).

Table 2. Summary of Carbon Stocks for the C-N and Carbon-Only Simulations, Showing Global Totals for Each Pool (PgC), With Percent of Total Global C Stock Shown in Parentheses^a

Experiment	Wood C ^b	Veg. C	CWD C ^c	Litter C	SOM C ^d	Total C
<i>Control</i>						
CN	613 (53)	653 (57)	147 (13)	16 (1)	334 (29)	1150
C	943 (47)	1014 (50)	247 (12)	28 (1)	736 (36)	2026
C _r	712 (49)	771 (53)	167 (11)	19 (1)	496 (34)	1452
<i>Years 1976–2000</i>						
CN+co2	649 (54)	690 (58)	153 (13)	16 (1)	339 (28)	1199
CN+ndep	619 (53)	660 (57)	149 (13)	16 (1)	339 (29)	1163
CN+co2ndep	656 (54)	698 (57)	155 (13)	17 (1)	344 (28)	1213
C+co2	1047 (48)	1125 (51)	269 (12)	31 (1)	776 (35)	2201
C _r +co2	803 (50)	870 (54)	184 (11)	22 (1)	537 (33)	1612
<i>Years 2076–2100</i>						
CN+co2	801 (57)	845 (60)	176 (13)	18 (1)	357 (26)	1397
CN+ndep	642 (53)	684 (57)	154 (13)	17 (1)	352 (29)	1206
CN+co2ndep	847 (57)	895 (60)	186 (13)	19 (1)	379 (26)	1480
C+co2	1527 (52)	1625 (55)	363 (12)	39 (1)	936 (32)	2963
C _r +co2	1225 (54)	1309 (57)	263 (12)	28 (1)	683 (30)	2284

^aValues are given for the final 25 a of the control experiments, and averaged over the periods 1976–2000 and 2076–2100 for the transient experiments.

^bWood component of vegetation (veg.) pool.

^cCoarse woody debris.

^dSoil organic matter (SOM), not including litter or coarse woody debris (CWD).

Fractions entering coarse woody debris are similar for the two models, and only very small fractions (1–2%) enter litter for either model. For the carbon-only model, partitioning of CO₂-fertilized carbon uptake is insensitive to changes in the model mean state induced by scaling V_{cmax} (experiments C + co2 versus C_r + co2).

[19] Nitrogen fertilization in the C-N model shifts partitioning of accumulated carbon away from vegetation pools and toward soil organic matter, compared to the CO₂ fertilization response. Partitioning of carbon to soil organic matter under N fertilization increased by a factor of three while partitioning to vegetation decreased by 29% com-

pared to that for CO₂ fertilization (experiments CN + ndep versus CN + co2), with little difference between historical and future periods (Table 4). Because the total carbon uptake due to N fertilization is 23–25% of that due to CO₂ fertilization, carbon partitioning in the combined CO₂ + N fertilization experiment is weighted toward the CO₂-fertilized pattern. Partitioning of carbon to coarse woody debris and litter are similar for CO₂, N, and CO₂ + N fertilization experiments.

[20] Next we consider the sensitivity of the land uptake to CO₂ concentration (β_L). Applying equation (1) in a moving window to 25-a segments of the time series for global mean

Table 3. Summary of Carbon Fluxes for the C-N and Carbon-Only Simulations, Showing Means With Interannual Standard Deviations in Parentheses^a

Experiment	GPP	NPP	AR	HR	Fire	NEE ^b
<i>Control</i>						
CN	102.1 (1.0)	41.6 (0.6)	60.5 (0.6)	40.6 (0.4)	1.1 (0.1)	0.01 (0.6)
C	177.5 (2.4)	79.0 (1.4)	98.5 (1.3)	76.6 (0.8)	2.4 (0.2)	−0.01 (1.5)
C _r	146.2 (1.7)	61.8 (1.0)	84.4 (0.9)	60.4 (0.5)	1.4 (0.1)	0.01 (1.2)
<i>Years 1976–2000</i>						
CN+co2	106.3 (1.2)	43.7 (0.7)	62.6 (0.7)	41.6 (0.4)	1.1 (0.1)	−0.96 (0.6)
CN+ndep	104.1 (1.0)	42.5 (0.6)	61.4 (0.6)	41.2 (0.4)	1.1 (0.1)	−0.20 (0.6)
CN+co2ndep	108.3 (1.3)	44.7 (0.7)	63.6 (0.7)	42.3 (0.5)	1.2 (0.1)	−1.24 (0.6)
C+co2	197.7 (4.4)	89.4 (2.4)	108.3 (2.2)	83.1 (1.5)	2.8 (0.2)	−3.62 (1.7)
C _r +co2	166.4 (3.9)	71.9 (2.0)	94.6 (2.0)	66.9 (1.3)	1.7 (0.1)	−3.25 (1.4)
<i>Years 2076–2100</i>						
CN+co2	118.8 (1.4)	49.9 (0.8)	68.9 (0.8)	45.8 (0.7)	1.3 (0.1)	−2.81 (0.6)
CN+ndep	109.0 (1.2)	44.9 (0.7)	64.0 (0.7)	43.1 (0.5)	1.2 (0.1)	−0.70 (0.6)
CN+co2ndep	127.9 (2.2)	54.5 (1.1)	73.4 (1.2)	49.0 (1.0)	1.5 (0.1)	−4.08 (0.6)
C+co2	256.5 (5.9)	120.3 (3.2)	136.2 (2.9)	105.7 (2.6)	4.0 (0.3)	−10.65 (2.0)
C _r +co2	220.5 (4.8)	99.4 (2.6)	121.2 (2.4)	87.5 (2.2)	2.6 (0.2)	−9.21 (1.6)

^aValues are given for the final 25 a of the control experiments, and over the periods 1976–2000 and 2076–2100 for the transient experiments. AR is autotrophic respiration. HR is heterotrophic respiration. NEE is net ecosystem exchange of carbon. NPP is net primary production. GPP is gross primary production. Units are PgC a^{−1}.

^bPositive upward (carbon release from land).

Table 4. Change in Land Carbon Stock (ΔC_{TOT} , PgC) and Its Percent Distribution in Various Pools, Under Increasing Atmospheric CO_2 and Increasing N Deposition, for Historical (1850–2000) and Future (2000–2100) Periods

Experiment	1850–2000					2000–2100				
	ΔC_{TOT}	% of ΔC_{TOT}				ΔC_{TOT}	% of ΔC_{TOT}			
		C_{VEG}	C_{CWD}	C_{LIT}	C_{SOM}		C_{VEG}	C_{CWD}	C_{LIT}	C_{SOM}
CN+co2	61.1	78	11	1	10	220.2	78	12	1	10
CN+ndep	15.6	55	11	2	32	50.3	56	12	1	31
CN+co2ndep	78.6	73	12	1	14	301.0	73	12	1	14
C+co2	223.3	64	11	2	24	843.1	66	13	1	20
C_r +co2	203.2	62	10	2	26	741.0	66	12	1	20

atmospheric CO_2 concentration and total ecosystem carbon, we find that β_L is lower by approximately a factor of four over the period 2000–2100 for the C-N model compared to the carbon-only model (Figure 2a). Both models show a decline in β_L which is accelerating over time. Potential mechanisms for this decline that could operate in both the carbon-only and C-N models include increasing rate of rise in atmospheric CO_2 concentration in the SRES A2 scenario in conjunction with constrained time constants for ecosystem response to CO_2 fertilization [Fung *et al.*, 2005], and approach to saturation in the leaf-scale photosynthetic CO_2 response [Wullschleger, 1993]. In the C-N model, this decline can also be partly attributed to increasing nitrogen limitation as both plant and heterotrophic nitrogen demands increase in response to CO_2 fertilization. Figure 2b shows that the ratio of β_L for experiments CN + co2:C + co2 gradually declines over this period, indicating the presence of additional mechanisms for declining β_L unique to the C-N model. The same figure shows that with the addition of N fertilization, the ratio of β_L for experiments CN + co2ndep:C + co2 increases over this period, supporting the interpre-

tation of increasing N limitation in CN + co2 that is being alleviated toward the end of the future scenario by N fertilization in CN + co2ndep. The modification of model mean state by imposing a 32% decrease of V_{cmax} in experiment C_r + co2 results in only a 13% decline in β_L at year 2100, compared to experiment C + co2 (Figure 2a), indicating that the large difference in β_L between CN + co2 and C + co2 is due mainly to factors other than the reduced mean state in CN + co2.

3.3. Response to Interannual Variation in Temperature and Precipitation

[21] Introduction of C-N coupling reduces the sensitivity of NEE to variation in temperature and precipitation (S_T and S_P , respectively). The sensitivity to temperature (S_T) is positive (warm anomalies associated with land carbon release) and the sensitivity to precipitation (S_P) is negative (wet anomalies associated with land carbon uptake) for both carbon-only and C-N models. The magnitudes of these sensitivities, however, are much smaller for the C-N model: S_T and S_P for the coupled carbon-nitrogen model (experi-

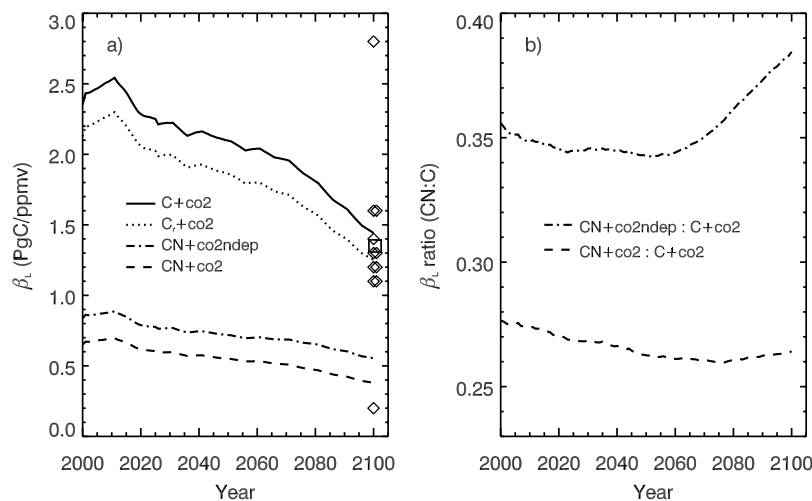


Figure 2. Comparison of β_L between C-N and carbon-only model configurations. (a) Trends in β_L for multiple experiments over the period 2000–2100. Symbols indicate values for eleven carbon-only models participating in C4MIP (diamonds) and the mean of the C4MIP models (square). C4MIP results from Friedlingstein *et al.* [2006]. (b) Trends in ratio of β_L between C-N and carbon-only model configurations over the period 2000–2100.

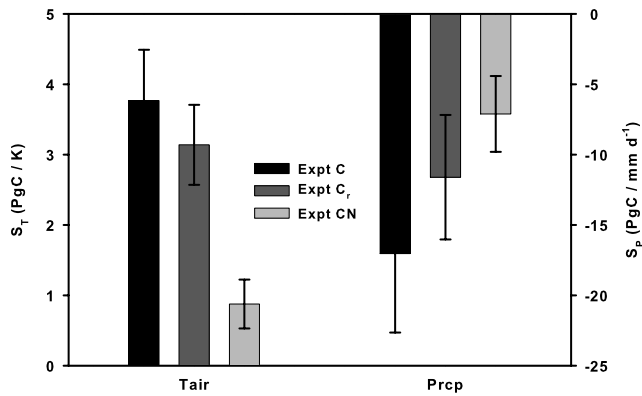


Figure 3. Sensitivity of global net ecosystem exchange of carbon (NEE) to interannual variability in global mean air temperature (Tair, S_T) and precipitation (Prctp, S_P) over land, estimated over the final 25 a of the control experiments. Error bars show 1 standard deviation around mean response.

ment CN) are 23% and 42%, respectively, of their values for the carbon-only model (experiment C, Figure 3). Precipitation explained $\sim 16\%$ of the interannual variance in global NEE for both model configurations, while temperature explained 37% for the carbon-only model and 14% with C-N coupling. Sensitivities to temperature and precipitation (S_T and S_P) were reduced in magnitude by 17% and 32%,

respectively, for the carbon-only model with reduced mean state compared to the default carbon-only model (experiments C_T versus C, Figure 3).

[22] There is considerable spatial variation in these responses for both carbon-only and coupled carbon-nitrogen models, with regions of positive and negative sensitivity to temperature (S_T , Figure 4a) and precipitation (S_P , Figure 4b). Spatial patterns for experiments CN and C are qualitatively similar, but the frequencies of large positive and negative values for the sensitivities (S_T and S_P) are reduced in CN. There is a general pattern of negative sensitivity to temperature (S_T) and positive sensitivity to precipitation (S_P) at higher latitudes ($>45^\circ$), shifting to positive S_T and negative S_P in the mid latitudes and tropics. The spatial patterns for sensitivity to precipitation (S_P) are similar to those found by *Doney et al.* [2006] for covariance between net land ecosystem carbon exchange and soil moisture in a long, stable control simulation from a fully coupled climate-carbon model.

[23] To address the mechanisms responsible for these spatial patterns, we disaggregated the NEE versus temperature and precipitation responses into independent responses for NPP, HR, and carbon loss due to fire. On the basis of comparisons of sign and magnitude we can say that NPP variability dominates the NEE response to temperature in most regions, reinforced in the tropics and subtropics by variability in fire (Figures 5a, 5b and 5d). HR variability dominates the temperature response in Scandinavia, central Asia, southeastern India, and parts of coastal northwestern North America (Figure 5c). The NPP

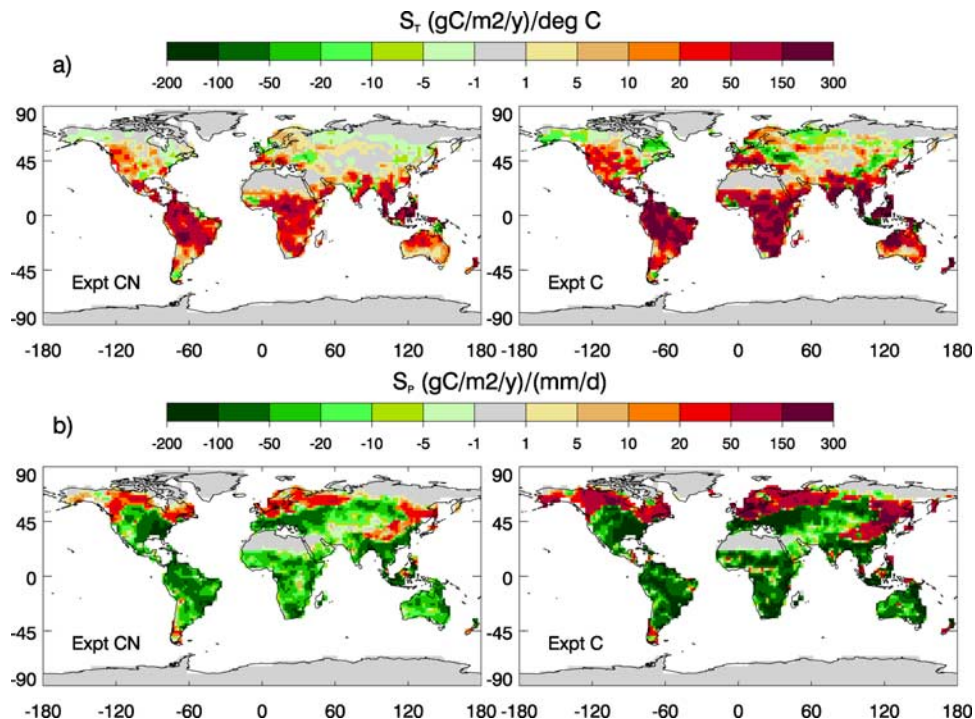


Figure 4. Sensitivity of NEE to (a) interannual variation in temperature (S_T), and (b) interannual variation in precipitation (S_P), calculated independently at each grid cell, using the final 25 a of the control simulations (experiments CN and C).

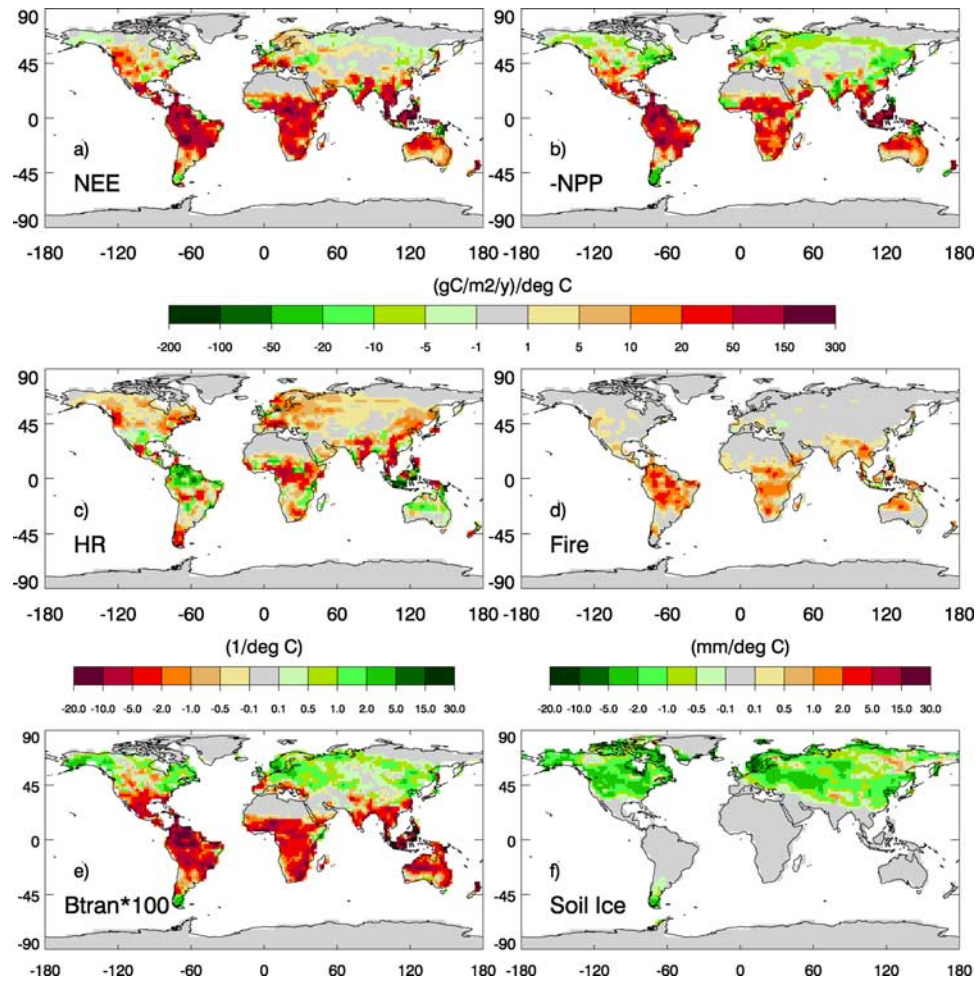


Figure 5. Dissection of NEE response to interannual variation in air temperature (T_{air}) from experiment CN, showing the regression slopes for various model outputs versus T_{air} , from multiple regressions against T_{air} and Prep. Color scales are arranged so that shades of green (red) indicate factors favoring carbon uptake (release) under warmer T_{air} (from Figure 4a, replicated here for ease of comparison). (a) NEE versus T_{air} , scaled by factor -1.0 to use a common color scale with other carbon fluxes. (b) NPP versus T_{air} , scaled by factor -1.0 to use a common color scale with other carbon fluxes. (c) Heterotrophic respiration (HR) versus T_{air} . (d) Fire flux versus T_{air} . (e) Btran versus T_{air} , scaled by factor 100.0 (see text for definition of Btran). (f) Soil ice versus T_{air} (total soil ice in first five soil layers, mm water equivalent). Figures 5a–5d share a color scale. Figures 5e and 5f show color scale and relevant units above map.

response is driven largely by variations in soil water availability, quantified here using the CLM biophysical variable Btran, which is the scaling factor (range 0–1) on stomatal conductance related to plant-available soil water. Warming in warm climates leads to soil drying (lower Btran, Figure 5e) due to high evaporative demand, while warming in cold climates is wetting the soil by melting soil ice (Figures 5e and 5f).

[24] NPP variability dominates the NEE response to precipitation in the tropics and mid latitudes, reinforced by variability in fire, with a clear shift to dominance by HR variability at high latitudes and in cold climates (Figure 6a–6d). The NPP response is driven directly by soil moisture (results not shown). The HR response in cold climates is partly explained by increased snow depth in anomalously

wet years (Figure 6e), which insulates the soil in winter and keeps soil temperature relatively high (Figure 6f), leading to increased soil respiration (Figure 6c).

3.4. Changes in Sensitivities to Temperature and Precipitation Under Future Scenarios of CO_2 and Nitrogen Deposition

[25] Introduction of C-N coupling reverses the sign of changes in sensitivity to both temperature and precipitation (S_T and S_P) over time under scenario of increasing CO_2 concentration. For experiment C + co_2 , global values for S_T and S_P around year 2100 increase in magnitude by 34% and 38%, respectively, compared to their 1850 values (Figure 7). That is, the value for sensitivity to temperature becomes more positive, and the value for sensitivity to precipitation

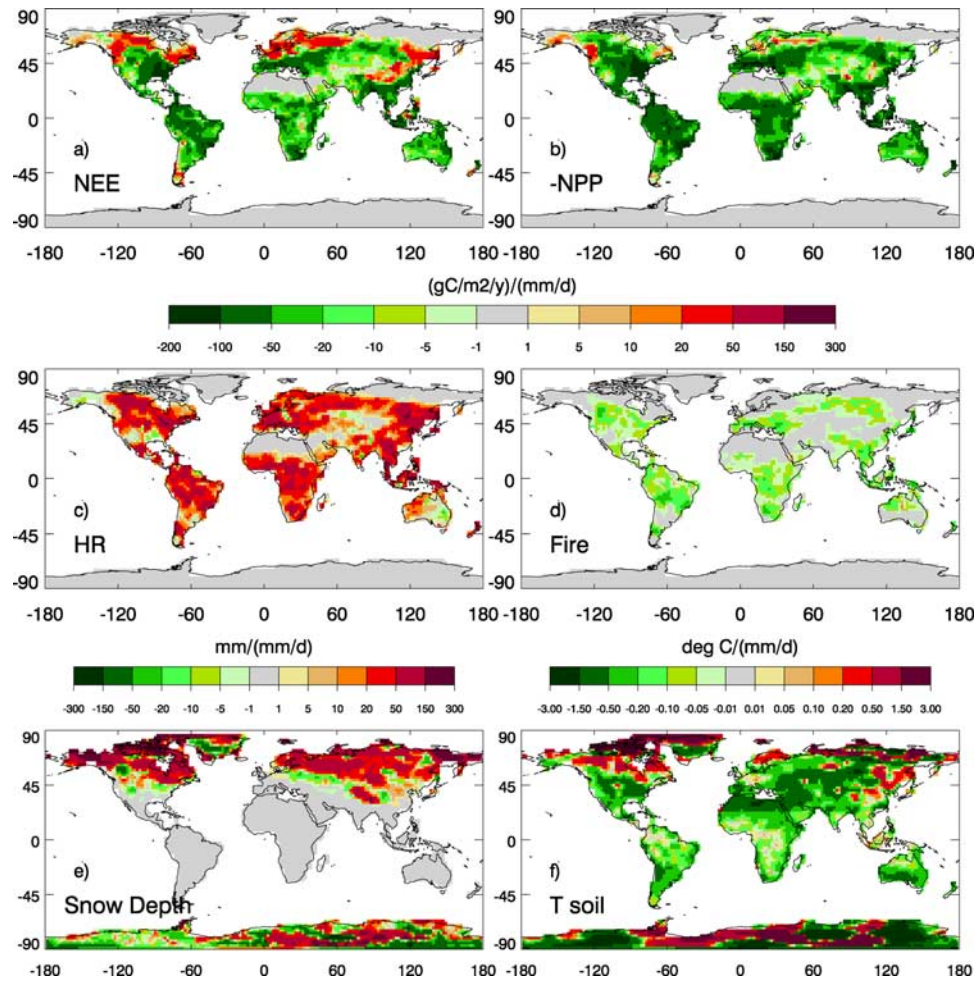


Figure 6. Dissection of NEE response to interannual variation in precipitation (Prcp) from experiment CN, showing the regression slopes for various model outputs versus Prcp, from multiple regressions against T_{air} and Prcp. Color scales are arranged so that shades of green (red) indicate factors favoring carbon uptake (release) under higher Prcp. (a) NEE versus Prcp (from Figure 4b, replicated here for ease of comparison). (b) NPP versus Prcp, scaled by factor -1.0 to use a common color scale with other carbon fluxes. (c) HR versus Prcp. (d) Fire flux versus Prcp. (e) Snow depth (mm) versus Prcp. (f) Soil temperature at ~ 20 cm depth (T_{soil}) versus T_{air} . Figures 6a–6d share a color scale. Figures 6e and 6f show color scale and relevant units above map.

becomes more negative. When carbon-nitrogen cycle coupling is included (experiment CN + co_2), S_T and S_P decreased in magnitude by 16% and 18%, respectively, over the same time period. When increased anthropogenic nitrogen deposition is included (experiment CN + co_2ndep), the change in S_T from 1850 to 2100 is smaller (7% decrease) and the change in S_P is larger (33% decrease) than for CO_2 increasing alone. We have not identified a mechanism explaining these differences in the transient responses to temperature and precipitation variation under increasing anthropogenic nitrogen deposition.

[26] In the carbon-only model configuration with reduced photosynthesis and increasing CO_2 (experiment $C_T + co_2$), changes in sensitivity to temperature and precipitation over time are in the same direction as for the default carbon-only model configuration (experiment $C + co_2$), with S_T and S_P

at year 2100 increasing in magnitude by 36% and 51%, respectively, compared to their 1850 values (Figure 7).

3.5. Measures of N Limitation

[27] Short-term N limitation can be assessed in terms of an instantaneous imbalance between supply and demand, which, when integrated over time, results in a long-term limitation expressed as a diminished ecosystem mean state and diminished nitrogen demand [Chapin *et al.*, 1986; Vitousek and Howarth, 1991]. We are able to estimate both instantaneous and long-term N limitation from our experiments. In the C-N experiments gross primary production prior to down-regulation by N limitation (referred to here as “potential GPP”) is calculated at each time step, allowing us to estimate instantaneous N limitation as the ratio of down-regulated GPP to potential GPP. In the carbon-only

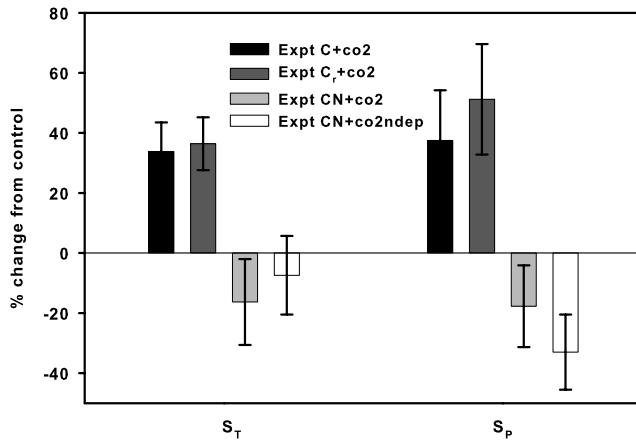


Figure 7. Changes in NEE sensitivity to interannual variation in air temperature (S_T) and precipitation (S_P) at year 2100 in simulations with increasing atmospheric CO_2 concentration, relative to S_T and S_P from the relevant control simulations (C, C_r , and CN). Values at 2100 are estimated from global total NEE and global mean temperature and precipitation over land for years 2076–2100.

experiments nitrogen limitation is eliminated by adding the nitrogen required to meet demand at each time step, allowing us to estimate long-term N limitation as the ratio of C-N (down-regulated) GPP to carbon-only GPP. These measures are expressed as scalars ranging from 0 to 1, with values closer to 0.0 indicating stronger N limitation.

[28] Instantaneous N limitation results in a 31% reduction in GPP, on the basis of down-regulated versus potential global total GPP in experiment CN. Long-term N limitation results in a 42% reduction in GPP, on the basis of comparison of global total GPP between experiments CN and C. Regional patterns differ substantially between instantaneous and long-term N limitation (Figure 8). In the boreal zone, for example, instantaneous limitation is weak and long-term limitation is strong, while in cold-dry and warm-wet regions both instantaneous and long-term limi-

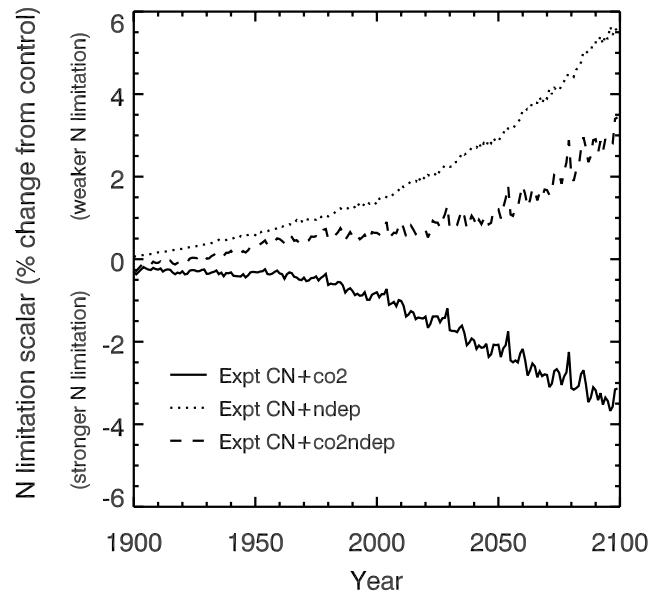


Figure 9. Changes in instantaneous N limitation scalar over the course of transient experiments, expressed as a percent change from N limitation in the C-N control, estimated from global total actual versus potential GPP.

tations tend to be weak. Changes in instantaneous N limitation in the transient experiments show progressively stronger N limitation under increasing atmospheric CO_2 (Figure 9, experiment CN + co_2). Increasing mineral nitrogen deposition has the expected effect of reducing overall N limitation (experiment CN + ndep), and the net effect of increasing CO_2 and increasing mineral nitrogen deposition is a reduction over time in global mean N limitation (experiment CN + co_2ndep). These transient changes are small, on the order of $\pm 5\%$, indicating that the global mean instantaneous N limitation is relatively stable on multihundred year timescales.

[29] The supplemental nitrogen input required in experiment C to completely eliminate N limitation for every land grid cell at every time step is 441 TgN a^{-1} , 4 times higher

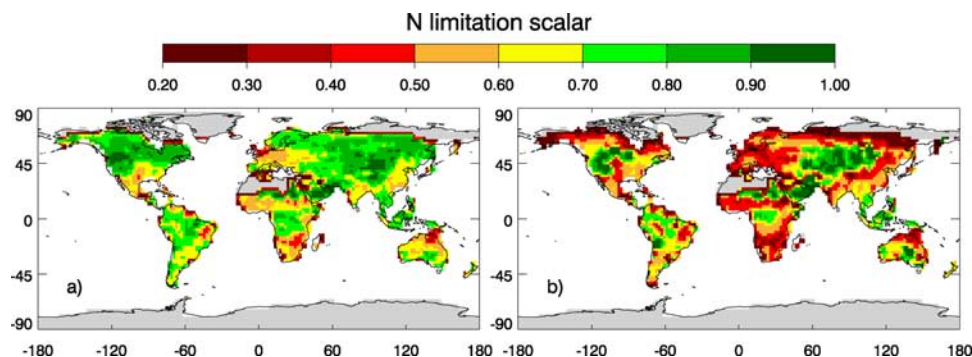


Figure 8. Spatial distribution of nitrogen limitation in the C-N control simulation, expressed as (a) instantaneous and (b) long-term limitation scalar (see section 3.5). Shades of red (green) show stronger (weaker) N limitation. Areas with gross primary production (GPP) $< 1 \text{ gC m}^{-2} \text{ a}^{-1}$ are shown in grey.

than the estimated nitrogen inputs from atmospheric deposition (6 TgN a^{-1}) and biological nitrogen fixation (104 TgN a^{-1}) in experiment CN. Total accumulation of nitrogen necessary to support the carbon accumulation in experiment C + co2 is 19.2 Pg nitrogen over the period 2000–2100. This is about 3 times higher than the high end of nitrogen accumulation estimated by *Hungate et al.* [2003] for this period on the basis of supply limitations. The total accumulation of nitrogen in experiment CN + co2ndep over this same period is 4.7 Pg nitrogen , which falls between the high and low estimates from *Hungate et al.* [2003], and represents an independent, mechanistic estimate of supply-limited nitrogen accumulation in land ecosystems over the coming century.

4. Discussion

4.1. Comparison to Observations and Previous Model Results

[30] Our results showing that accumulation of carbon in soil organic matter is higher and accumulation in vegetation carbon is lower for N fertilization compared with CO_2 fertilization are consistent with findings from recent observational studies. In labeled N tracer studies for forests in Europe and North America, *Nadelhoffer et al.* [2004, 1999] have shown that most tracer N is recovered in soil organic matter ($\sim 80\%$), with little recovery in tree biomass (3%–17%, depending on tissue). In a meta-analysis of the influence of CO_2 and nitrogen fertilization across multiple ecosystem types, *van Groenigen et al.* [2006] found that elevated CO_2 leads to accumulation of soil C and N only when N is added at rates well above background atmospheric inputs. Several studies have shown that CO_2 fertilization tends to shift N away from soil organic matter and into plant biomass, which, given the higher C:N for biomass versus soil organic matter, is associated with a preferential increase in vegetation carbon [*Gill et al.*, 2006; *Hungate et al.*, 2006; *Luo et al.*, 2006].

[31] The issue of fractionation in carbon uptake between vegetation and soil pools is important since these pools can have very different residence times and are affected differently by disturbances such as fire and forest harvest. *Dufresne et al.* [2002] note that there is a factor of 2 difference in the ratio of carbon stored in vegetation to that stored in soil organic matter because of increasing CO_2 between the land components of two coupled climate-carbon cycle models, with the IPSL model storing carbon preferentially in vegetation (ratio $\sim 2:1$), while the Hadley model stores preferentially in soil organic matter (ratio $\sim 1:2$). Our results show carbon storage due to increasing CO_2 strongly weighted toward vegetation, with a ratio of $\sim 8:1$ for CO_2 fertilization, dropping to $\sim 5:1$ when N fertilization is included.

[32] Our estimate of present-day carbon sink due to anthropogenic mineral nitrogen deposition (0.24 PgC a^{-1} for the period 1981–2000) is in reasonable agreement with several independent estimates. *Field et al.* [1992] used simple stoichiometric logic to provide a range of recent N-fertilized uptake of $0.3\text{--}2.5 \text{ PgC a}^{-1}$, and suggested that the correct value is likely closer to the low end of that range.

Nadelhoffer et al. [1999] used a simple budget based on a synthesis of studies in temperate forests to estimate a current global forest-only uptake of 0.25 PgC a^{-1} due to anthropogenic N fertilization. In a modeling study, *Holland et al.* [1997] give a significantly higher range for the estimated N-fertilized carbon sink, $\sim 0.7\text{--}2.0 \text{ PgC a}^{-1}$. Most of the models included in the nitrogen deposition intercomparison of *Lamarque et al.* [2005] did not have a representation of ammonia atmospheric chemistry, and so the model-generated N deposition data set used in our study does not include ammonia deposition. Since this component represents more than 50% of the present-day total N deposition [*Dentener et al.*, 2006], it is likely that our current estimate is biased low.

[33] In a recent synthesis of observed influence of increasing CO_2 on NPP in temperate forests, *Norby et al.* [2005] found a consistent increase in NPP of $\sim 23\%$ for CO_2 about 200 ppmv higher than ambient ($\sim 550 \text{ ppmv}$) across a broad productivity range. We find an increase in global NPP at present compared to preindustrial steady state of 7% ($\sim 100 \text{ ppmv}$ increase in CO_2), and a 22% increase in NPP at year 2100 relative to present ($\sim 460 \text{ ppmv}$ increase in CO_2). Our results are not directly comparable to the experimental findings, since the experiments impose a step change in CO_2 while our results are from transient simulations, for which a smaller response is expected.

[34] Declining β_L under increasing CO_2 observed in our transient experiments for both carbon-only and C-N models (Figure 2a) is similar in pattern and mechanism to results from *Fung et al.* [2005] for a fully coupled climate-carbon cycle model with a carbon-only land biogeochemistry component. Our estimates of β_L at 2100 from carbon-only experiments C + co2 and C_r + co2 (1.4 and $1.2 \text{ PgC ppmv}^{-1}$, respectively) are similar to the results from *Fung et al.* [2005] ($1.1 \text{ PgC ppmv}^{-1}$), and very close to the mean β_L from the eleven models participating in the recent C4MIP intercomparison ($1.35 \text{ PgC ppmv}^{-1}$, Figure 2a) [*Friedlingstein et al.*, 2006]. This suggests that reductions in β_L similar to those observed between our carbon-only and C-N model might also be obtained from the addition of explicit C-N coupling in other models.

[35] The global stock of vegetation C in experiment CN + co2ndep (ca. 2000) is in good agreement with recent estimates, but the total soil organic matter carbon stock is significantly lower than current estimates [*Houghton et al.*, 2001]. As described previously [*Thornton, 1998; Thornton and Rosenbloom, 2005*], the converging cascade model of litter and soil organic matter dynamics used here can be parameterized with either three or four soil organic matter pools, with equivalent fidelity to data from radio-labeled substrate decomposition experiments. Additional experiments showed that the vegetation states and carbon uptake transient responses to increasing atmospheric CO_2 and nitrogen deposition are affected very little by the choice of three or four soil organic matter pools (differences generally $< 2\%$, results not shown). The total soil organic matter stock when using the four-pool model is approximately twice as large, in better general agreement with inventory-based estimates [*Houghton et al.*, 2001], and so

we recommend that future simulations use the four-pool model configuration.

4.2. Influence of Model Mean State

[36] Our analysis of the influence of mean state is intended to address the pragmatic question of whether it would be adequate to substitute a simpler model formulation to capture the main C-N induced climate-carbon cycle responses. If changes in fundamental carbon-climate responses induced by a simple alteration of the carbon cycle mean state in the carbon-only model are similar to the changes obtained by the introduction of full prognostic C-N coupling, then an argument could be made for avoiding the added complexity of the C-N coupling mechanisms, instead parameterizing the C-N coupling effects as a down-regulation of mean rates of photosynthesis. Conversely, an argument can be made for explicitly including the C-N coupling if the responses to altered mean state and added C-N mechanisms differ in ways that are likely to be important for the purposes of a particular model application. Here we are specifically concerned with model applications in the context of a fully coupled carbon cycle-climate simulation for projection of future climate on timescales of several hundred years.

[37] The relative importance of model mean state on the finding of greatly reduced land carbon uptake sensitivity to atmospheric CO₂ concentration (β_L) in the C-N compared to carbon-only model (Figure 2a) can be assessed by comparing some indicators of mean state, such as vegetation carbon and GPP, with differences in β_L between models C, C_r and CN. Since the mean states for C_r and CN are not the same, we normalize responses by comparing the changes in mean state relative to C. Reductions in vegetation carbon and GPP, compared to C, are 1.5 and 2.3 times larger, respectively, for CN than for C_r. We therefore expect that if the effect on β_L of introducing C-N coupling is mainly due to the effect of N limitation on the model mean state, then the ratio of differences in β_L between CN and C_r should fall close to the range 1.5–2.3. In fact the ratio of differences in β_L (at year 2000) is 6.6, several times larger than the range for mean state differences. This suggests that most of the difference in β_L between models CN and C is due not to the reduced mean state in CN, but to more fundamental C-N coupling mechanisms. Results are similar when considering model behavior at year 2100.

[38] The same analysis applied to steady state estimates of land carbon cycle sensitivity to interannual variation in temperature and precipitation (S_T and S_P , Figure 3) suggests that C-N coupling mechanisms play an important role in the C-N model response to temperature, but that the differences between carbon-only and C-N model in response to precipitation could be due mainly to differences in the model mean state. For the case of changes in S_T and S_P over time under the influence of rising atmospheric CO₂ concentration, the influence of C-N coupling (CN + co2 versus C + co2 in Figure 7) has the opposite sign compared to the influence of reduced mean state in the carbon-only model (C_r versus C in Figure 7). This is a strong indication that the difference in temporal dynamics of S_T and S_P between the C-N and carbon-only models is not primarily due to

different mean states. We conclude that for the β_L and S_T responses, as well as for the temporal dynamics of the S_P response, the behavior of the C-N model cannot be adequately captured through simple down-regulation of photosynthesis in the carbon-only model.

4.3. Model Limitations and Future Directions

[39] The CLM-CN configuration described here has several significant shortcomings. First, these simulations have not considered the influence of changing land cover and land use on C-N cycle dynamics. Disturbance history has been shown to have a strong influence on carbon and nitrogen cycle dynamics in previous observational studies [Bautista-Cruz and del Castillo, 2005; Gholz et al., 1985; Law et al., 2003; Prober et al., 2005; Torn et al., 2005] and modeling studies [Bond-Lamberty et al., 2005; Bugmann and Solomon, 2000; Schimel et al., 1997; Thonicke et al., 2001; Thornton et al., 2002; Turner et al., 2007]. Without an explicit treatment of disturbance history it is difficult to assess the behavior of the model against historical observations of atmospheric CO₂ concentration, since an important part of that signal is due to carbon sources and sinks from vegetation disturbance, land management practices, and regrowth. This capability is currently being added to the model, and future studies will report on the influence of these dynamics on the climate-carbon response mechanisms discussed here.

[40] While the current model includes a detailed treatment of many components of the terrestrial nitrogen cycle, it lacks detail on the processes of nitrification, denitrification, and volatilization, all of which are important components of the long-term nitrogen balance. The vertical distribution of nitrogen cycling processes in the soil column is not treated explicitly, in part because of large uncertainties associated with these processes, compounded by uncertainties in the treatment of vertical soil water dynamics. This prevents an explicit treatment of speciation of mineral nitrogen between ammonium and nitrate. More sophisticated models for these processes are available [e.g., Li et al., 2005; Neff and Asner, 2001], but considerable work is required to integrate the existing knowledge within the biophysical and biogeochemical framework of CLM-CN. Development in this direction is underway now.

[41] While the current model includes the fundamental controls on fire from fuels and climate, there has not yet been any systematic evaluation of the model behavior against observations. The transport of fire emissions is also not treated prognostically in our fully coupled system, although there is evidence that long-range transport from large biomass burning sources could play an important role in C-N dynamics [Fabian et al., 2005].

[42] The current treatment of biological nitrogen fixation is entirely empirical, and has an important influence on the long-term establishment of the C-N model mean state. We found that model response to increasing CO₂ is not particularly sensitive to the parameterization of this process (results not shown), but a more mechanistic treatment of the process would help to address uncertainties in the detailed spatial patterns of N limitation. The results presented here will also be sensitive to the details of the

modeled N deposition fields [Lamarque et al., 2005]. We are exploring the effects of replacing the MOZART-2 inputs with results from other models, from the work of Lamarque et al. [2005] and/or Dentener et al. [2006]. In the future we plan to have a prognostic nitrogen deposition capability operational within the fully coupled CCSM framework.

[43] Finally, the current model ignores potential limitations from other nutrients. Phosphorus limitation, in particular, is known to play an important role in tropical forests growing on highly weathered soils [Vitousek and Howarth, 1991] as well as in some temperate systems [Gosz et al., 1973], and there are also potentially important interactions between the phosphorus cycle and biological nitrogen fixation [Vitousek et al., 2002]. We note that, even for systems where phosphorus limitation is more important than nitrogen limitation, the inclusion of nitrogen dynamics will produce a result that is closer to reality than a carbon-only model. However, because of the critical role of the tropical forests in establishing the past, present, and future trajectories of the global carbon cycle and climate-carbon cycle interactions, we must very soon confront the challenge of developing a parsimonious treatment of carbon-nitrogen-phosphorus coupling for use in global coupled climate system modeling.

5. Conclusions

[44] We tested the hypothesis that inclusion of explicit prognostic coupling between the carbon and nitrogen cycles in the land biogeochemistry component of a coupled climate system model has important consequences for climate-carbon cycle interactions. We found that, in comparison to a carbon-only model configuration, the most critical mechanisms controlling the sign and magnitude of feedbacks between the global climate system and the terrestrial biosphere are significantly altered by the introduction of an explicit prognostic treatment of the nitrogen cycle. Specifically:

[45] 1. Sensitivity of land carbon uptake to increasing atmospheric CO₂ concentration is smaller by a factor of 3.6 for C-N versus carbon-only model configurations, with a shift for the C-N model toward proportionally more carbon uptake in vegetation and less in soil organic matter. Total carbon uptake due to increasing atmospheric CO₂ over the period 2000–2100 is smaller by a factor of 3.8 for the C-N versus carbon-only model.

[46] 2. Land carbon cycle responses to interannual variation in both temperature and precipitation have significantly smaller magnitudes for the C-N model, compared to its carbon-only counterpart: globally integrated responses are smaller by factors of 4.3 and 2.4 for temperature and precipitation, respectively.

[47] 3. Under the influence of rising atmospheric CO₂ concentration, land carbon cycle sensitivities to interannual variation in temperature and precipitation are shown to decrease in magnitude over time for the C-N model, while increasing in magnitude over time for the carbon-only counterpart.

[48] 4. The influence of model mean state does not appear to explain the large decrease in sensitivity to

CO₂, the smaller sensitivity to temperature variation, or the transient changes in temperature and precipitation sensitivity under increasing CO₂ that result from introduction of C-N coupling.

[49] We conclude that introduction of terrestrial C-N coupling is likely to have a fundamental impact on the climate-carbon cycle feedbacks in a fully coupled climate-biogeochemistry simulation. We further conclude that a simple reparameterization of a carbon-only model to produce an altered mean state resembling that obtained under explicit C-N coupling is not likely to result in climate-carbon cycle dynamics similar to those obtained under the explicit C-N coupled system. C-N coupling is certain to reduce the direct CO₂ fertilization effect in a coupled simulation, producing a tendency toward higher atmospheric CO₂ concentrations for identical fossil fuel emissions scenarios. The complex spatial patterns of land carbon cycle response to temperature and precipitation variation suggest that the strength and sign of the globally integrated carbon-climate feedbacks will depend on the convolution of these patterns with the spatial patterns of climate change resulting from a particular model or ensemble member. Investigations of climate-carbon cycle feedback mechanisms using CLM-CN as a component of a fully coupled climate-carbon system model are now underway.

[50] **Acknowledgments.** We thank S. Doney, D. Schimel, G. Bonan, and E. Holland for helpful discussions, and we thank two anonymous reviewers for their thoughtful and constructive comments on the manuscript. This work was supported in part by NASA Earth Science Enterprise, Terrestrial Ecology program, grant W19,953 to P. E. Thornton. Additional support was provided by the National Center for Atmospheric Research (NCAR) through the NCAR Community Climate System Modeling program, and through the NCAR Biogeosciences program. NCAR is sponsored by the National Science Foundation.

References

- Bautista-Cruz, A., and R. F. del Castillo (2005), Soil changes during secondary succession in a tropical montane cloud forest area, *Soil Sci. Soc. Am. J.*, *69*, 906–914.
- Betts, R. A. (2005), Integrated approaches to climate-crop modelling: Needs and challenges, *Philos. Trans. R. Soc., Ser. B.*, *360*, 2049–2065.
- Bonan, G. B. (1990), Carbon and nitrogen cycling in North American boreal forests: II. Biogeographic patterns, *Can. J. For. Res.*, *20*, 1077–1088.
- Bonan, G. B., and S. Levis (2006), Evaluating aspects of the Community Land and Atmosphere Models (CLM3 and CAM3) using a dynamic global vegetation model, *J. Clim.*, *19*, 2290–2301.
- Bond-Lamberty, B., S. T. Gower, D. E. Ahl, and P. E. Thornton (2005), Reimplementation of the Biome-BGC model to simulate successional change, *Tree Physiol.*, *25*, 413–424.
- Bousquet, P., P. Peylin, P. Ciais, C. Le Quere, P. Friedlingstein, and P. P. Tans (2000), Regional changes in carbon dioxide fluxes of land and oceans since 1980, *Science*, *290*, 1342–1346.
- Bugmann, H., and A. M. Solomon (2000), Explaining forest composition and biomass across multiple biogeographical regions, *Ecol. Appl.*, *10*, 95–114.
- Chapin, F. S., P. M. Vitousek, and K. Van Cleve (1986), The nature of nutrient limitation in plant communities, *Am. Naturalist*, *127*, 48–58.
- Ciais, P., et al. (2005), Europe-wide reduction in primary productivity caused by the heat and drought in 2003, *Nature*, *437*, 529–533.
- Collins, W. D., et al. (2006), The Community Climate System Model Version 3 (CCSM3), *J. Clim.*, *19*, 2122–2143.
- Dentener, F., et al. (2006), Nitrogen and sulfur deposition on regional and global scales: A multi-model evaluation, *Global Biogeochem. Cycles*, *20*, GB4003, doi:10.1029/2005GB002672.
- Dickinson, R. E., K. W. Oleson, G. B. Bonan, F. M. Hoffman, P. Thornton, M. Vertenstein, Z.-L. Yang, and X. Zeng (2006), The Community Land Model and its climate statistics as a component of the Community Climate System Model, *J. Clim.*, *19*, 2302–2324.

- Doney, S. C., K. Lindsay, I. Fung, and J. John (2006), Natural variability in a stable, 1000-yr global coupled climate-carbon cycle simulation, *J. Clim.*, *19*, 3033–3054.
- Dufresne, J.-L., L. Fairhead, H. Le Treut, M. Berthelot, L. Bopp, P. Ciais, and P. Monfray (2002), On the magnitude of positive feedback between future climate change and the carbon cycle, *Geophys. Res. Lett.*, *29*(10), 1405, doi:10.1029/2001GL013777.
- Fabian, P., M. Kohlpaintner, and R. Rollenbeck (2005), Biomass burning in the Amazon-fertilizer for the mountainous rain forest in Ecuador, *Environ. Sci. Pollut. Res.*, *12*, 290–296.
- Feddema, J., K. W. Oleson, G. B. Bonan, L. O. Mearns, L. E. Buja, G. A. Meehl, and W. M. Washington (2005), The importance of land-cover change in simulating future climates, *Science*, *310*, 1674–1678.
- Field, C. B., F. S. Chapin III, P. A. Matson, and H. A. Mooney (1992), Responses of terrestrial ecosystems to the changing atmosphere: A resource-based approach, *Annu. Rev. Ecol. Systemat.*, *23*, 201–235.
- Friedlingstein, P., J.-L. Dufresne, P. M. Cox, and P. Rayner (2003), How positive is the feedback between climate change and the carbon cycle?, *Tellus, Ser. B*, *55*, 692–700.
- Friedlingstein, P., et al. (2006), Climate-carbon cycle feedback analysis: results from the C⁴MIP model intercomparison, *J. Clim.*, *19*, 3337–3353.
- Fung, I. Y., S. C. Doney, K. Lindsay, and J. John (2005), Evolution of carbon sinks in a changing climate, *Proc. Natl. Acad. Sci. U. S. A.*, *102*, 11,201–11,206.
- Gholz, H. L., C. S. Perry, W. P. Cropper Jr., and L. C. Hendry (1985), Litterfall, decomposition, and nitrogen and phosphorous dynamics in a chronosequence of slash pine (*Pinus elliottii*) plantations, *For. Sci.*, *31*, 463–478.
- Gill, R. A., L. J. Anderson, H. W. Polley, H. B. Johnson, and R. B. Jackson (2006), Potential nitrogen constraints on soil carbon sequestration under low and elevated atmospheric CO₂, *Ecology*, *87*, 41–52.
- Gosz, J. R., G. E. Likens, and F. H. Bormann (1973), Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire, *Ecol. Monogr.*, *43*, 173–191.
- Goulden, M. L., J. W. Munger, S.-M. Fan, B. C. Daube, and S. Wofsy (1996), Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability, *Science*, *271*, 1576–1578.
- Holland, E. A., et al. (1997), Variations in the predicted spatial distribution of atmospheric nitrogen deposition and their impact on carbon uptake by terrestrial ecosystems, *J. Geophys. Res.*, *102*, 15,849–15,866.
- Horowitz, L. W., et al. (2003), A global simulation of tropospheric ozone and related tracers: Description and evaluation of MOZART, version 2, *J. Geophys. Res.*, *108*(D24), 4784, doi:10.1029/2002JD002853.
- Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson (Eds.) (2001), *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*, 881 pp., Univ. of Cambridge Press, Cambridge, UK.
- Hungate, B. A., J. S. Dukes, R. Shaw, Y. Luo, and C. B. Field (2003), Nitrogen and climate change, *Science*, *302*, 1512–1513.
- Hungate, B. A., et al. (2006), Nitrogen cycling during seven years of atmospheric CO₂ enrichment in a scrub oak woodland, *Ecology*, *87*, 26–40.
- Lamarque, J. F., et al. (2005), Assessing future nitrogen deposition and carbon cycle feedbacks using a multi-model approach: Analysis of nitrogen deposition, *J. Geophys. Res.*, *110*, D19303, doi:10.1029/2005JD005825.
- Law, B. E., O. J. Sun, J. Campbell, S. Van Tuyl, and P. E. Thornton (2003), Changes in carbon storage and fluxes in a chronosequence of ponderosa pine, *Global Change Biol.*, *9*, 510–514.
- Li, C. S., S. Frolking, and K. Butterbach-Bahl (2005), Carbon sequestration in arable soils is likely to increase nitrous oxide emissions, offsetting reductions in climate radiative forcing, *Clim. Change*, *72*, 321–338.
- Luo, Y., et al. (2004), Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide, *Bioscience*, *54*, 731–739.
- Luo, Y., D. Hui, and D. Zhang (2006), Elevated CO₂ stimulates net accumulations of carbon and nitrogen in land ecosystems: a meta-analysis, *Ecology*, *87*, 53–63.
- McGuire, A. D., J. M. Melillo, L. A. Joyce, D. W. Kicklighter, A. L. Grace, B. Moore III, and C. J. Vorosmarty (1992), Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America, *Global Biogeochem. Cycles*, *6*, 101–124.
- McGuire, A. D., et al. (2001), Carbon balance of the terrestrial biosphere in the twentieth century: analyses of CO₂, climate and land use effects with four process-based ecosystem models, *Global Biogeochemical Cycles*, *15*, 183–206.
- Miller, H. G. (1986), Carbon x nutrient interactions: The limitations to productivity, *Tree Physiol.*, *2*, 373–385.
- Moorhead, D. L., J. F. Reynolds, and W. G. Whitford (1986), A conceptual model for primary productivity, decomposition and nitrogen cycling in the Chihuahuan creosotebush desert, *Tree Physiol.*, *2*, 215–222.
- Nadelhoffer, K. J., B. A. Emmett, P. Gunderson, O. J. Kjønaas, C. J. Koopmans, P. Schleppi, A. Tietema, and R. F. Wright (1999), Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests, *Nature*, *398*, 145–148.
- Nadelhoffer, K. J., B. P. Colman, W. S. Currie, A. Magill, and J. D. Aber (2004), Decadal-scale fates of ¹⁵N tracers added to oak and pine stands under ambient and elevated N inputs at the Harvard Forest (USA), *For. Ecol. Manage.*, *196*, 89–107.
- Nakicenovic, N., and R. Swart (Eds.) (2000), *Special Report on Emissions Scenarios*, 612 pp., Cambridge Univ. Press, Cambridge, UK.
- Neff, J. C., and G. P. Asner (2001), Dissolved organic carbon in terrestrial ecosystems: Synthesis and a model, *Ecosystems*, *4*, 29–48.
- Norby, R. J., et al. (2005), Forest response to elevated CO₂ is conserved across a broad range of productivity, *Proc. Natl. Acad. Sci.*, *102*, 18,052–18,056.
- Oleson, K. W., et al. (2004), Technical description of the Community Land Model (CLM), 174 pp., *NCAR Tech. Note, NCAR-TN-461+STR*, Natl. Cent. for Atmos. Res., Boulder, Colo.
- Pastor, J., and W. M. Post (1988), Response of northern forests to CO₂-induced climate change, *Nature*, *334*, 55–58.
- Prior, S. A., G. B. Runion, R. J. Mitchell, H. H. Rogers, and J. S. Amthor (1997), Effects of atmospheric CO₂ on longleaf pine: productivity and allocation as influenced by nitrogen and water, *Tree Physiol.*, *17*, 397–405.
- Prober, S. M., K. R. Thiele, I. D. Lunt, and T. B. Koen (2005), Restoring ecological function in temperate grassy woodlands: Manipulating soil nutrients, exotic annuals and native perennial grasses through carbon supplements and spring burns, *J. Appl. Ecol.*, *42*, 1073–1085.
- Rastetter, E. B., M. G. Ryan, G. R. Shaver, J. M. Melillo, K. J. Nadelhoffer, J. E. Hobbie, and J. D. Aber (1991), A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO₂, climate and N deposition, *Tree Physiol.*, *9*, 101–126.
- Rastetter, E. B., G. I. Agren, and G. R. Shaver (1997), Responses of N-limited ecosystems to increased CO₂: A balanced-nutrition, coupled-element-cycles model, *Ecol. Appl.*, *7*, 444–460.
- Reich, P. B., S. E. Hobbie, T. Lee, D. S. Ellsworth, J. B. West, D. Tilman, J. M. H. Knops, S. Naeem, and J. Trost (2006), Nitrogen limitation constrains sustainability of ecosystem response to CO₂, *Nature*, *440*, 922–925.
- Santiago, L. S., E. A. G. Schuur, and K. Silvera (2005), Nutrient cycling and plant-soil feedbacks along a precipitation gradient in lowland Panama, *J. Trop. Ecol.*, *21*, 461–470.
- Schimel, D. S., W. J. Parton, C. V. Cole, D. S. Ojima, and T. G. F. Kittel (1990), Grassland biogeochemistry: Links to atmospheric processes, *Clim. Change*, *17*, 13–25.
- Schimel, D. S., et al. (1997), Continental scale variability in ecosystem processes: Models, data, and the role of disturbance, *Ecol. Monogr.*, *67*, 251–271.
- Tans, P. P., I. Y. Fung, and T. Takahashi (1990), Observational constraints on the global atmospheric CO₂ budget, *Science*, *247*, 1431–1438.
- Thornicke, K., S. Venevsky, S. Sitch, and W. Cramer (2001), The role of fire disturbance for global vegetation dynamics: Coupling fire into a dynamic global vegetation model, *Global Ecol. Biogeogr.*, *10*, 661–667.
- Thornton, P. E. (1998), Regional ecosystem simulation: combining surface- and satellite-based observations to study linkages between terrestrial energy and mass budgets, Ph.D. thesis, 280 pp, Univ. of Montana, Missoula.
- Thornton, P. E., and N. A. Rosenbloom (2005), Ecosystem model spin-up: Estimating steady state conditions in a coupled terrestrial carbon and nitrogen cycle model, *Ecol. Modell.*, *189*, 25–48.
- Thornton, P. E., et al. (2002), Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests, *Agric. For. Meteorol.*, *113*, 185–222.
- Thornton, P. E., and N. E. Zimmermann (2007), An improved canopy integration scheme for a land surface model with prognostic canopy structure, *J. Clim.*, *20*, 3902–3923.
- Thornton, P. E., R. B. Cook, B. H. Braswell, B. E. Law, W. M. Post, H. H. Shugart, B. T. Rhyne, and L. A. Hook (2005), Archiving numerical models of biogeochemical dynamics, *Eos Trans. AGU*, *86*, 431–432.
- Torn, M. S., P. M. Vitousek, and S. E. Trumbore (2005), The influence of nutrient availability on soil organic matter turnover estimated by incubations and radiocarbon modeling, *Ecosystems*, *8*, 352–372.

- Turner, D. P., W. D. Ritts, J. M. Styles, Z. Yang, W. B. Cohen, B. E. Law, and P. E. Thornton (2007), A diagnostic carbon flux model to monitor the effects of disturbance and interannual variation in climate on regional NEP, *Tellus, Ser. B*, *58*, 476–490.
- van Groenigen, K.-J., J. Six, B. A. Hungate, M. A. de Graaff, N. van Breemen, and C. van Kessel (2006), Element interactions limit soil carbon storage, *Proc. Natl. Acad. Sci.*, *103*, 6571–6574.
- Vitousek, P. M., and R. W. Howarth (1991), Nitrogen limitation on land and in the sea: How can it occur?, *Biogeochemistry*, *13*, 87–115.
- Vitousek, P. M., et al. (2002), Towards an ecological understanding of biological nitrogen fixation, *Biogeochemistry*, *57/58*, 1–45.
- Wahren, C. H. A., M. D. Walker, and M. S. Bret-Harte (2005), Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment, *Global Change Biol.*, *11*, 537–552.
- Washington, W. M., et al. (2000), Parallel climate model (PCM) control and transient simulations, *Clim. Dyn.*, *16*, 755–774.
- Wullschleger, S. D. (1993), Biochemical limitations to carbon assimilation in C₃ plants: A retrospective analysis of the A/Ci curves from 109 species, *J. Exp. Bot.*, *44*, 907–920.
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