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S. Zaehle, A. Friend, P. Friedlingstein, F. Dentener, P. Peylin, et al.. Carbon and nitrogen cycle dynamics in the O-CN land surface model: 2. Role of the nitrogen cycle in the historical terrestrial carbon balance. *Global Biogeochemical Cycles*, 2010, 24 (1), pp.n/a-n/a. 10.1029/2009GB003522 . hal-03201208

HAL Id: hal-03201208

<https://hal.science/hal-03201208v1>

Submitted on 18 Apr 2021

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Carbon and nitrogen cycle dynamics in the O-CN land surface model: 2. Role of the nitrogen cycle in the historical terrestrial carbon balance

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Received 24 March 2009; revised 12 August 2009; accepted 24 August 2009; published 11 February 2010.

[1] Global-scale results of the new O-CN terrestrial biosphere model coupling the carbon (C) and nitrogen (N) cycles show that the model produces realistic estimates of present-day C and N stocks and fluxes, despite some regional biases. N availability strongly affects high-latitude foliage area and foliage N, limiting vegetation productivity and present-day high-latitude net C uptake. Anthropogenic N deposition is predicted to have increased net primary productivity due to increases in foliage area and foliage N, contributing 0.2–0.5 Pg C yr⁻¹ to the 1990s global net C uptake. While O-CN's modeled global 1990s terrestrial net C uptake (2.4 Pg C yr⁻¹) is similar to the estimate not accounting for anthropogenic N inputs and N dynamics (2.6 Pg C yr⁻¹), its latitudinal distribution and the sensitivity of the terrestrial C balance to its driving factors are substantially altered by N dynamics, with important implications for future trajectories of the global carbon cycle.

Citation: Zaehle, S., A. D. Friend, P. Friedlingstein, F. Dentener, P. Peylin, and M. Schulz (2010), Carbon and nitrogen cycle dynamics in the O-CN land surface model: 2. Role of the nitrogen cycle in the historical terrestrial carbon balance, *Global Biogeochem. Cycles*, 24, GB1006, doi:10.1029/2009GB003522.

1. Introduction

[2] Land surface processes such as evapotranspiration and net carbon (C) exchanges with the atmosphere play a pivotal role in the dynamics of the Earth system. Much research effort in recent years has been oriented toward the understanding and quantification of the role of these processes in the dynamics of the terrestrial C cycle and the future evolution of its net balance [Cramer *et al.*, 2001; Prentice *et al.*, 2001; Friedlingstein *et al.*, 2006]. Despite an increased understanding of the global terrestrial carbon budget and its persistent net C uptake, the relative contribution of different mechanisms to the evolution of the land carbon balance and their geographical variation remains highly uncertain [House *et al.*, 2003]. A lack of understanding of the mechanisms controlling the net land-atmosphere C flux is hampering accurate projections of the future evolution of the terrestrial C balance and is contributing strongly to the large uncertainty in coupled carbon-cycle climate simulations [Friedlingstein *et al.*, 2006].

[3] One commonly missing factor in current models of terrestrial carbon dynamics is the nitrogen (N) cycle. N is an

essential component of enzymes and structural proteins, nucleic acids, pigments, and other secondary metabolites [van Oijen and Levy, 2004]. Molecular nitrogen is an extremely stable compound, requiring large amounts of energy to reduce it to ammonia and hence make it available to biological systems [Houlton *et al.*, 2008]. Therefore, despite its atmospheric abundance, N is a key limiting factor for growth in many pristine temperate and boreal ecosystems, and thus important for the geographic distribution of vegetation productivity [Vitousek and Howarth, 1991], composition, and structure. As a consequence, plant tissue N is often highly correlated with key metabolic rates such as photosynthesis [Field and Mooney, 1986] and respiration [Sprugel *et al.*, 1996], and an important control on the turnover of soil organic matter [Anderson, 1973; Flanagan and van Cleve, 1983].

[4] Understanding the role of the terrestrial N cycle in the Earth system is essential for answering many of the major outstanding questions concerning the future evolution of the terrestrial carbon balance. This is largely because the capacity of the terrestrial biosphere to store C in response to elevated atmospheric CO₂ concentrations ([CO₂]) is limited by ecosystem nitrogen availability and the C:N stoichiometry of plant tissue [Hungate *et al.*, 2003; Luo *et al.*, 2004]. However, the magnitude of this N limitation on C sequestration is poorly quantified [Luo *et al.*, 2006]. A further area of uncertainty concerns the net effect of any warming on the terrestrial C balance. Increased soil organic matter decomposition resulting from future higher soil temperatures could, while causing loss of soil C through increased respiration, increase net N mineralization and thereby enhance plant productivity [Melillo *et al.*, 2002]. One study has even found that increased N availability with

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climate change could completely reverse the predicted net C losses due to increased plant growth [Thornton *et al.*, 2007]. Furthermore, geographically widespread increases in anthropogenic atmospheric N deposition have been suggested to have contributed to the measured imbalance in the recent terrestrial C cycle [Gruber and Galloway, 2008]. However, there is no consensus as to the importance of such a contribution or its potential future effects on terrestrial carbon dynamics [Magnani *et al.*, 2007; Sutton *et al.*, 2008]. Finally, the use of N fertilizer has dramatically increased over the last 6 decades to boost agricultural production, dramatically modifying cropland C and N cycles [Galloway *et al.*, 2004].

[5] Despite the importance of the terrestrial N cycle, only few of the global terrestrial biosphere models (TBMs) used for carbon cycle studies have accounted for aspects of terrestrial nitrogen dynamics [McGuire *et al.*, 1992; Woodward *et al.*, 1995; Friend *et al.*, 1997]. Notably, none of the land surface schemes representing terrestrial carbon cycling to simulate climate-carbon feedbacks to predict future climate change used in the IPCC's fourth assessment report account for N dynamics [Denman *et al.*, 2007]. This situation is now rapidly changing, since some of the existing N cycle TBMs have recently been integrated into climate model land surface schemes [Thornton *et al.*, 2007; Sokolov *et al.*, 2008]. The cause for the missing representation resides both in the capacity of carbon cycle models to successfully reproduce benchmarks of the present-day global C cycle [Prentice *et al.*, 2000] and in the complexity of the terrestrial nitrogen cycle, comprising numerous transformation processes with multiple climatic, edaphic, and biological controls on the turnover and partitioning of N toward plants and soils, and on losses to leaching and trace gas emissions. The development of such models is further complicated by uncertainties in our quantitative understanding of the global terrestrial nitrogen cycle and suitable observations to rigorously evaluate key processes in a global N cycle model [Gruber and Galloway, 2008].

[6] To better understand the past and quantify future dynamics of the terrestrial carbon balance, we have developed a new version of the land surface scheme used by the IPSL-CM4 coupled general circulation model [Marti *et al.*, 2005], ORCHIDEE [Krinner *et al.*, 2005], that includes representations of the key processes of the terrestrial N cycle. The model, hereafter referred to as O-CN, is described in detail in an accompanying paper [Zaehle and Friend, 2010]. O-CN contains representations of the effects of N availability on photosynthetic capacity (including leaf area) and respiration rates, plant and community structure, and soil organic matter decomposition, as well as N losses to leaching and nitrification-denitrification related N emissions, and considers reactive N inputs from biological N fixation, atmospheric deposition, and fertilizer applications. Key innovations with respect to other recent global N model approaches [e.g., Thornton *et al.*, 2007; Xu-Ri and Prentice, 2008] are that N concentrations in vegetation and soil are prognostic state variables, plant allocation is sensitive to plant N content, and canopy and soil processes operate at a half-hourly time step, permitting simulation of rapid shifts in process rates such as denitrification peaks following rain

events, as well as allowing for a mechanistic coupling between terrestrial and atmospheric processes.

[7] Zaehle and Friend [2010] provide an in-depth evaluation of O-CN for European temperate and boreal forest ecosystems, where sufficient observations are available to characterize carbon and nitrogen dynamics. They show that the model gives satisfactory estimates of seasonal and annual C and N fluxes along a gradient of climate and N deposition. The present paper expands this analysis to the global scale and evaluates its capacity to simulate realistic estimates of the present-day geographic distribution of terrestrial C and N cycles. A thorough quantitative evaluation of a global nitrogen cycle model is far from straightforward because of the scarcity of relevant observations on, for example, net N mineralization, N leaching, and N trace gas losses at the global scale [Galloway *et al.*, 2004]. We rely on compilation of the literature on global N stocks and fluxes, and in addition exploit the tight coupling between the terrestrial C and N cycles to infer the global performance of O-CN from comparisons to robust observables of the carbon cycle, with a focus on the marginal effect of N constraints. In addition to the use of a database of observed site-level gross and net primary productivity covering all major biomes, we rely on the use of atmospheric CO₂ concentration ([CO₂]) measurements at several remote monitoring stations [GLOBALVIEW-CO₂, 2007], both through direct comparison using a forward atmospheric transport model and, with the aim of reducing transport modeling uncertainty, land-atmosphere net C flux estimates from an ensemble of inversions of atmospheric [CO₂] [Baker *et al.*, 2006]. Atmospheric [CO₂] measurements integrate regional net surface-atmosphere CO₂ fluxes and therefore provide an additional constraint on the magnitude of terrestrial C cycling, particularly at northern high latitudes where the observed atmospheric signal is dominated by terrestrial sources and sinks [Heimann *et al.*, 1998].

[8] Finally, we use O-CN to quantify the effect of accounting for nitrogen cycle dynamics on the simulated magnitudes and geographical distribution of the historical terrestrial C balance, focusing on the interactions of terrestrial N cycling with increasing atmospheric [CO₂], N deposition, and N fertilizer application, as well as concurrent climatic changes.

2. Methods

2.1. Model

[9] O-CN is developed from the land surface scheme of the IPSL-CM4 coupled atmosphere-ocean-land general circulation model [Marti *et al.*, 2005], ORCHIDEE, described by Krinner *et al.* [2005], and has been extended through representation of key nitrogen cycle processes. O-CN simulates the terrestrial energy, water, carbon, and nitrogen budgets for discrete tiles (i.e., fractions of the grid cell) occupied by up to 12 plant functional types (PFTs) [see Krinner *et al.*, 2005] from diurnal to decadal time scales. The model can be run on any regular grid and is applied here at a spatial resolution of 2° × 2°. The model has been conceived as a land surface scheme and links a soil-vegetation-atmosphere transfer scheme, dealing with energy

Table 1. Model Experiments Performed With O-CN, Indicating the Years Used for Specific Forcings^a

Model Experiment	Atmospheric [CO ₂]	Climate	N Deposition	N Fertilizer
S1	All 1860–2002	1860–2002	1860–2002	1860–2002
<i>Simulation Excluding One Factor</i>				
S2	All-Nfert (= All')	1860–2002	1860–2002	1860
S3	All'-CO ₂	1860	1860–2002	1860–2002
S4	All'-climate	1860–2002	1901–1910	1860–2002
S5	All'-N deposition	1860–2002	1860–2002	1860
<i>Simulation Including Only One Factor</i>				
S6	CO ₂	1860–2002	1901–1910	1860
S7	Climate	1860	1860–2002	1860
S8	N deposition	1860	1901–1910	1860–2002

^aThe climate data set [Mitchell *et al.*, 2004] does not contain observations prior to 1901, thus the years 1901–1910 were repeated (random draws) for simulation periods prior to 1901.

and water fluxes [Ducoudré *et al.*, 1993], to representations of short- and long-term carbon cycling [Viivy, 1996] and vegetation structure [Sitch *et al.*, 2003]. As described by Zaehle and Friend [2010], several modifications to the original model were necessary to facilitate the inclusion of the N cycle. These changes are (1) representation of canopy photosynthesis based on the work of Friend and Kiang [2005] that explicitly accounts for foliage N controls on leaf-level photosynthesis and its integration to canopy-scale carbon and water fluxes; (2) dynamic calculation of the annual maximum foliage area by replacing the original C allocation scheme [Friedlingstein *et al.*, 1999] with allometric constraints accounting for the costs of the growth of a unit of area of foliage due to the requirement of supporting root and shoot tissues [Shinozaki *et al.*, 1964]; (3) treatment of labile and reserve plant C pools to improve modeling of seasonal phenology and to buffer against C shortages during high respiration and low productivity; and (4) consideration of tree population dynamics as functions of population density, growth-dependent establishment and mortality [Sitch *et al.*, 2003] in ORCHIDEE's static mode, in which vegetation composition is prescribed externally.

[10] We refer to the modified ORCHIDEE model, i.e., including the above changes, as O-C and use this version to quantify the effects of the added model complexity through the coupling the terrestrial carbon and nitrogen cycles on the contemporary state of the terrestrial carbon cycle and its evolution in time. O-C shares biogeophysical, biogeochemical, and vegetation dynamics process representations with O-CN, but does not explicitly account for N constraints on productivity and allocation patterns. Tissue N concentrations are maintained at mean observed levels (see Zaehle and Friend [2010] for values used) at each time step by allowing plants to satisfy their N demand by accessing all mineral N not required to meet the current N demand of litter decomposition. When this amount of available mineral soil N failed to meet the plant N demand, N is added directly to the plants to meet the remaining demand.

[11] Nitrogen cycling in O-CN is described in detail by Zaehle and Friend [2010]. The main features are

(1) prognostic plant tissue N concentrations; (2) N control on leaf-level photosynthesis and plant respiration; (3) nutrient status-dependent allocation to different plant organs (e.g., controls on belowground investment and maximum foliage area); (4) fine root mass-dependent plant N uptake; (5) N control on soil organic matter decomposition and N mineralization rate, based on the CENTURY model [Parton *et al.*, 1993; Kirschbaum and Paul, 2002]; and (6) half-hourly leaching and gaseous N losses resulting from nitrification and denitrification processes in the soil, adapted from Li *et al.* [2000].

2.2. Modeling Protocol

[12] Descriptions of the modeling protocol and the forcing data used are given as Text S1.¹ From model equilibrium in terms of preindustrial carbon and nitrogen stocks and fluxes, a transient simulation was performed using observed historical changes in atmospheric [CO₂], climate, N deposition, and N fertilization over the period 1860–2002 (simulation S1; see Table 1). These results are used in sections 3.1 and 3.2 for the evaluation of the modeled present-day C and N cycles. The marginal contribution of one of these time-dependent factors to the present state of the C and N cycles was determined by two methods, to allow assessment of the degree of synergistic effects between the factors (Table 1; results in section 3.3). Synergies may arise because of the complex interactions between the carbon and nitrogen cycles, for example, due to the alleviation of the N limitation on the response to increased atmospheric [CO₂] from concurrent increases in N availability. The marginal contribution including the synergistic effects of the covarying factors was determined in a set of four simulations (S2 to S5), each with one time-dependent factor held constant at a time. The “simple” marginal effect of the historical changes in atmospheric [CO₂], climate, and N deposition was inferred by simulations varying only one time-dependent factor at a time (simulations S6–S8). We report results for the total land, including croplands and the N fertilizer treatment, but note that estimates of soil C storage in croplands are likely to be overestimates due to the simple representation of crop management in the current version of O-CN. Key data sets used to benchmark O-CN are described in Text S2.

3. Results

[13] In section 3.1, key components of the global simulated N and C cycles are compared to observation-based estimates with the aim of establishing the degree to which O-CN produces realistic estimates of recent terrestrial C and N stocks and fluxes. Section 3.2 focuses on the effects of introducing the N cycle constraint into C cycle modeling. In section 3.3, O-CN is employed to evaluate the consequences of explicitly accounting for N dynamics on the simulation of terrestrial carbon cycle dynamics in the historical period. Supplementary material is available for this paper (Tables S1–S5 and Figures S1–S8), describing spatial patterns and biome-wise estimates of vegetation and soil

¹Auxiliary materials are available in the HTML. doi:10.1029/2009GB003522.

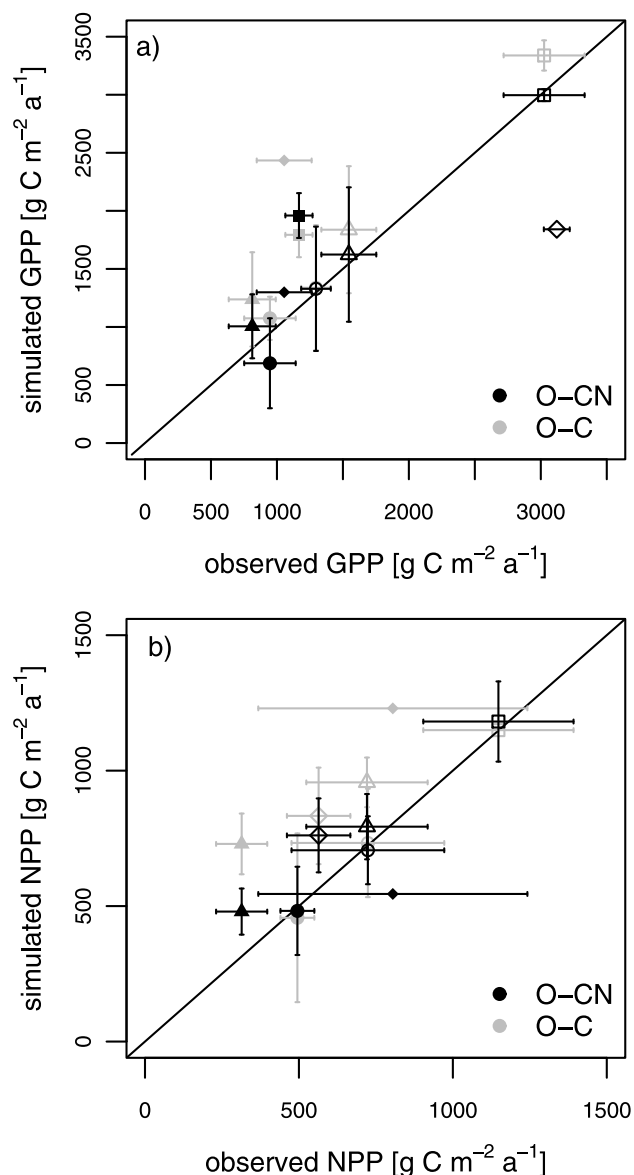


Figure 1. Mean annual (a) GPP (gross primary productivity) and (b) NPP (net primary productivity) of eight global vegetation types based on observations from a total of 99 (GPP) and 159 (NPP) sites [Luyssaert *et al.*, 2007] and simulated 1990s average GPP and NPP for each of these sites. Error bars denote the between-site standard deviation of observations and model, respectively. Vegetation types are tropical broadleaved evergreen (open squares, TrBE), tropical broadleaved raingreen (open diamonds, TrBR), temperate needleleaved evergreen (open triangles, TeNE), temperate broadleaved evergreen (closed squares, TeBE), temperate broadleaved summergreen (open circles, TeBS), boreal needleleaved evergreen (closed triangles, BNE), boreal broadleaved summergreen (closed circles, BBS), and boreal needleleaved summergreen (closed diamonds, BNS). See Table S3 for details.

C and N pools and major C and N fluxes, statistics of model-data comparisons, and additional information for Figures 1–4 and 6.

3.1. Evaluation of Simulated Modern Global Carbon and Nitrogen Cycles C and N Stocks in Vegetation and Soil

[14] O-CN predicts a global vegetation C stock of 537 Pg C for the 1990s, with biomass densities ranging from $<0.2 \text{ kg C m}^{-2}$ in sparsely vegetated tundra and arid shrublands to about 33 kg C m^{-2} in tropical rain forests. These estimates are in general agreement with inventory-based estimates (Table 2), albeit with a low biased model-based boreal forest biomass estimate. Global soil C stock for the 1990s is estimated to be 1289 Pg C, close to the central estimate (1272 Pg C) of Post *et al.* [1985], but at the lower end of the range of previously reported estimates (700–3000 Pg C) [Post *et al.*, 1982; Zinke *et al.*, 1998]. Soil organic carbon densities range from zero in deserts to $>50 \text{ kg C m}^{-2}$ in boreal forests.

[15] Simulated 1990s global vegetation N stock is 3.8 Pg N (Table 2). This estimate is comparable to a recent modeling study using the LPJ-DGVM (5.3 Pg N) [Xu-Ri and Prentice, 2008]. However, the latter estimate refers to potential natural vegetation and thus does not account for croplands, likely overestimating present-day vegetation N stocks by 0.9 Pg N. Average N density in vegetation is 24 g N m^{-2} , reaching a maximum of about 230 g N m^{-2} in tropical rain forests. Lumped vegetation C:N ratios range from around 30 for grasslands, 132 for subtropical forests, 150 for temperate deciduous forests, to 210 for boreal evergreen forests (reaching a maximum of 270), falling within the ranges reported for forest vegetation (115, 155, and 210, respectively) by Vitousek *et al.* [1988].

[16] Simulated global soil N storage is 101 Pg N, remarkably close to the data-based estimate (95 Pg N) of Post *et al.* [1985]. The average organic N density in soils is 763 g N m^{-2} , reaching a maximum of more than 4000 g N m^{-2} in Siberian needleleaved evergreen forests. Soil C:N ratios range between a minimum of 8 in agricultural fields to 31 in boreal forests, with a global mean of about 13. These values agree fairly well with mean values of the global soil database of Zinke *et al.* [1998].

3.1.1. C Cycling

[17] Average gross and net primary productivity (GPP and NPP, respectively) for the different PFTs of O-CN compare favorably with field-based estimates in the database of Luyssaert *et al.* [2007] (Figure 1), with root-mean-squared errors of $338 \text{ g C m}^{-2} \text{ yr}^{-1}$ (GPP) and $153 \text{ g C m}^{-2} \text{ yr}^{-1}$ (NPP). GPP and NPP estimates by major global biomes agree well with published observational and modeling studies (Tables 2, S1, and S3), with the exception of an apparent high bias in boreal productivity, despite the good fit to site-level data in Figure 1. GPP and NPP simulated for each boreal location of the database, as shown in Figure 1, are biased high relative to the simulated global area-weighted means for each PFT, suggesting that these locations, and potentially also the observations, may not be truly representative for boreal productivity.

[18] Atmospheric $[\text{CO}_2]$ measurements at stations of the GLOBALVIEW network provide a regionally integrated

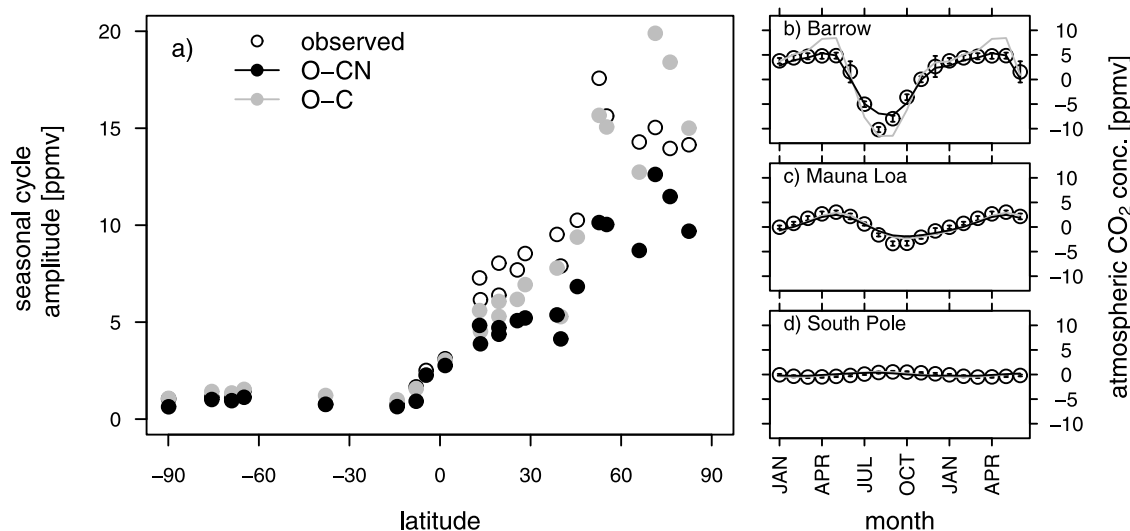


Figure 2. (a) Mean 1990s observed and simulated amplitude of the seasonal cycle of atmospheric [CO₂] at 24 stations of the Globalview network [GLOBALVIEW-CO₂, 2007], as well as mean simulated and observed seasonal cycles at three selected stations: (b) Point Barrow (Alaska, United States), (c) Mauna Loa (Hawaii, United States), and (d) South Pole. Error bars are the standard deviation of the monthly observations.

constraint on net land-atmosphere CO₂ exchanges to further assess O-CN's simulated C cycling. O-CN reproduces the observed northward increase in the amplitude of the seasonal cycle (Figure 2a), when transporting the simulated net land CO₂ fluxes of O-CN within one particular atmospheric transport model (see Table S4). However, there is a systematic tendency to underestimate the rate of this increase. The simulated phase of atmospheric [CO₂] matches the observations with time differences for the minimal concentrations smaller than 1 month for most of the 24 monitoring stations. Figures 2b–2d illustrate the observed mean seasonal cycles (1991–2000) of atmospheric [CO₂] at a high-latitude (Point Barrow, Alaska, United States), a tropical (Mauna Loa, Hawaii, United States), and a southern station (South Pole). These results are generally confirmed by a comparison of the seasonal cycle in net land-atmosphere CO₂ flux over large terrestrial regions to the ensemble of flux estimates based on inversions of atmospheric [CO₂] concentration measurements (Figure S3) using 13 different transport models from the TransCom 3 project [Baker *et al.*, 2006]. This comparison eliminates, at least partially, the potential bias due to the choice of one particular transport model and few sampling stations.

3.1.2. N Cycling

[19] Global annual rates of plant N uptake (1126 Tg N yr⁻¹, or 8.6 g N m⁻² yr⁻¹, Table 2) are comparable to estimates from other global nitrogen cycle models (1073–1084 Tg N yr⁻¹) [Melillo *et al.*, 1993; Xu-Ri and Prentice, 2008]. Mean N plant uptake rates range from close to zero g N m⁻² yr⁻¹ in deserts, to 4 in boreal forests, 8 in temperate broadleaved forest, 13 in tropical forests, and up to 30 g N m⁻² yr⁻¹ in tropical grasslands. The spatial patterns of plant N uptake, as well as of vegetation productivity, follow closely those of net N mineralization, the primary control on plant N availability. Intensively managed croplands with

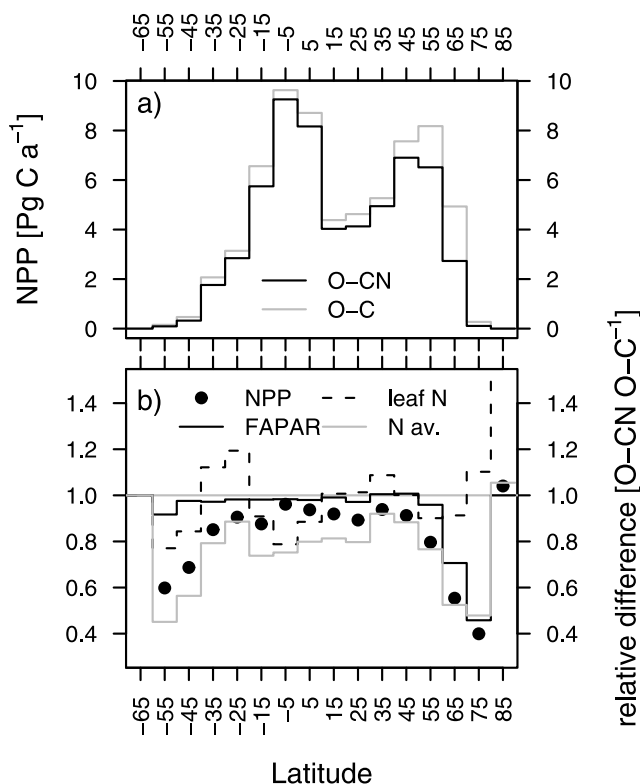


Figure 3. Latitudinal distribution of (a) mean 1990s NPP simulated by O-CN and O-C, as well as (b) the ratios of annual plant N supply (net N mineralization + biological N fixation + N deposition: N av.), fraction of absorbed photosynthetically active radiation (FAPAR), and foliage N concentrations between O-CN and O-C (O-CN/O-C).

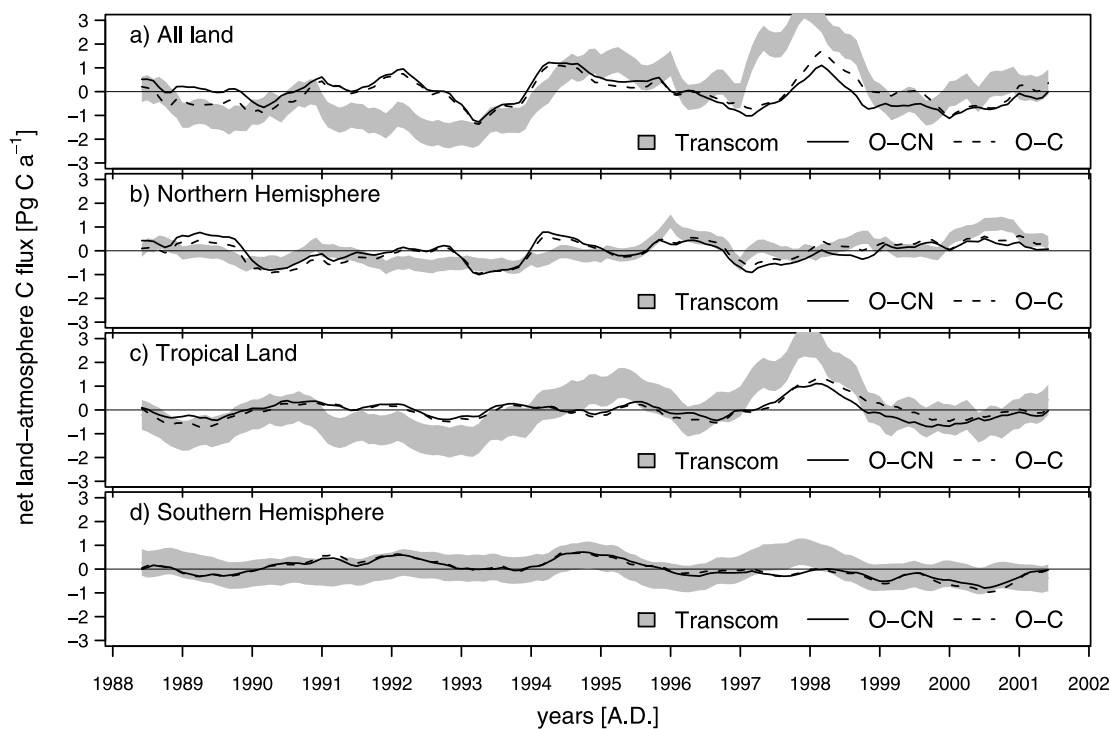


Figure 4. Interannual variability of the net land-atmosphere C exchanges (1988–2002) for (a) global, (b) northern extratropical, (c) tropical, and (d) southern extratropical land regions. The time series are 12 months running mean with the mean seasonal cycle removed. The gray area indicates the mean \pm standard deviation of the Transcom3 inversion study [Baker et al., 2006]. The Transcom3 study used 13 atmospheric transport models, observed time series of atmospheric $[\text{CO}_2]$ at 78 stations, and the average seasonal net terrestrial and ocean CO_2 fluxes as prior estimates, as well as a seasonal wind field.

a high N input from fertilizer application are an exception to this pattern. The global N uptake rate implies a nutrient use efficiency (NPP/N uptake) of 52, which is close to the value of around 50 suggested by Schlesinger [1991] and obtained by the TEM model [Melillo et al., 1993].

[20] Global N leaching is estimated to be 86 Tg N yr^{-1} , of which the majority (57 Tg N yr^{-1}) is related to fertilizer application in croplands. This estimate is larger than previous estimates of riverine N export to coastal shelves ($40\text{--}60 \text{ Tg N yr}^{-1}$) and inland lakes (11 Tg N yr^{-1}) based on transport modeling [Boyer et al., 2006b]. However, the two estimates may not be incompatible when considering the loss of some of the N leached below the rooting zone to denitrification along the hydrological pathway before reaching the continental shelf or inland waters [Galloway et al., 2004]. Such losses are not accounted for in our model and may contribute to our higher estimate. It is also likely that uncertainty in the modeling of the amount, form, and timing of the fertilizer application also contributes to our relatively high estimate. The leaching rate from natural ecosystems (29 Tg N yr^{-1}) is compatible with leaching estimates discounting for inputs from artificial fertilizer (27 Tg N yr^{-1}) [Galloway et al., 2004].

[21] Simulated global emissions of NO_x from soils average $26.8 \text{ Tg N yr}^{-1}$, which is comparable to the estimate obtained by Davidson and Kinglerlee [1997] based on extrapolating local soil emission measurements (21 Tg N yr^{-1}). However, this value is double the mean estimate of the

natural soil NO_x source in data compilations for atmospheric chemistry modeling ($5\text{--}12 \text{ Tg N yr}^{-1}$) [Denman et al., 2007]. This difference could probably be reconciled by accounting for more rapid turnover of surface layer NO_x through processes such as recapture of emitted NO_x within the canopy [Ganzeveld et al., 2002], currently not modeled in O-CN.

[22] Global N_2O emissions are estimated to be 7.0 Tg N yr^{-1} , which is at the lower end of the range derived from bottom-up and top-down estimates based on the atmospheric N_2O budget ($4.2\text{--}14 \text{ Tg N yr}^{-1}$) [Olivier et al., 1998; Denman et al., 2007]. Simulated agricultural emissions alone amount to 2.1 Tg N yr^{-1} , agreeing well with estimates from bottom-up modeling ($1.9\text{--}2.1 \text{ Tg N yr}^{-1}$) [Olivier et al., 1998; Stehfest, 2005]. Our lower total N_2O emission rate is due primarily to a low N_2O source within the tropics. The first study to invert atmospheric N_2O concentrations to obtain regional source and sink estimates using the atmospheric transport model TM3 [Hirsch et al., 2006] suggested a substantial source of N_2O in the tropics ($5.2\text{--}8.0 \text{ Tg N yr}^{-1}$), larger than the tropical land source estimate of $4.4 \pm 0.2 \text{ Tg N yr}^{-1}$ simulated by O-CN. Nevertheless, simulated mean N_2O emissions from natural tropical ecosystems (0.7 ; range: $0.1\text{--}2.7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) fall within the range of the small number of estimates ($0.2\text{--}1.4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) based on daily to weekly site-scale observations in the database of Stehfest and Bouwman [2006]. By far the largest gaseous N flux is that of molecular N ($64.2 \text{ Tg N yr}^{-1}$). This

Table 2. Mean 1990s Global Stocks and Fluxes of C and N, Estimated by O-C and O-CN, as Well as Observation-Based Estimates^a

	O-C	O-CN	Literature
GPP ^b (Pg C yr ⁻¹)	148.4	132.6	90–160
NPP ^c (Pg C yr ⁻¹)	65.9	57.5	59.9–62.6
Net land-atmosphere C flux ^d (Pg C yr ⁻¹)	-2.62	-2.38	-4.8 to -1.6
Vegetation C ^e (Pg C)	647.1	537.0	560–652
Soil C ^e (Pg C)	1723.1	1288.7	700–3000
N uptake (Tg N yr ⁻¹)	1436.8	1126.9	
Vegetation N (Pg N)	5.0	3.8	
Soil N ^e (Pg N)	138.8	100.0	95.0
NO _x emission ^f (Tg N yr ⁻¹)	35.0	26.8	21
N ₂ O emission ^g (Tg N yr ⁻¹)	8.7	7.0	4.2–14
Total N emission (Tg N yr ⁻¹)	121.7	98.2	
Total N leaching ^h (Tg N yr ⁻¹) (natural/agricultural)	58.1/85.2	19.9/57.1	51–71

^aEstimates by biomes are given in Tables S1 and S2.

^bKnorr and Heimann [1995] and Ciais et al. [1997].

^cSaugier and Roy [2001].

^dHouse et al. [2003].

^ePost et al. [1985].

^fDavidson and Kingerlee [1997].

^gOlivier et al. [1998] and Denman et al. [2007].

^hBoyer et al. [2006b].

simulated N₂ flux is 30% lower than the flux calculated by balancing the terrestrial inputs and outputs of reactive N by Galloway et al. [2004], mainly because of our higher estimates of losses to riverine transport and NO_x emission.

3.2. Influence of N Feedbacks on the Present-Day C Cycle

[23] Both versions of the model, with (O-CN) and without (O-C) explicitly considering terrestrial N dynamics, produce estimates of global productivity and C storage in vegetation and soil commensurate with current understanding (Table 2). However, O-CN simulated vegetation productivity (Figure 3a), and in consequence biomass, are lower in the boreal zone, which in turn leads to a shallower seasonal cycle of the net land-atmosphere CO₂ flux in comparison to the O-C version (Figure 2). The reason for this is that simulated N availability is about 50% lower in the boreal zone when explicitly accounting for the nitrogen constraint on the terrestrial C cycle (O-CN) than the N availability diagnosed from O-C (Figure 3b). The higher productivity in O-C compensates for the too shallow amplitude of the seasonal cycle in O-CN when compared with atmospheric data, leading instead to an overestimation of the amplitude at the northernmost stations by O-C (Figure 2).

[24] Despite these differences, the deseasonalized variability of the net land-atmosphere flux is very similar between O-C and O-CN (Figure 4). That is, N dynamics do not strongly alter magnitude or phasing of the interannual variability (IAV) of the net of land-atmosphere C flux. The magnitude of the modeled variability in northern extratropical land, where most of the change in the seasonal cycle is located, is comparable to that obtained by a study using 13 different inverse atmospheric transport models [Baker et al., 2006]. This approach integrates the observed

IAV in atmospheric [CO₂] at 78 monitoring stations using average seasonal prior estimates of terrestrial and ocean net C fluxes and seasonal wind fields. While key characteristics of the IAV can be identified using the inverse approach [Peylin et al., 2005], uncertainty in the inverse estimate due to prior estimates and wind fields is likely to be at least 0.2 Pg C yr⁻¹ larger the range between 13 transport models, as shown in Figure 4 [Baker et al., 2006]. Small model-inversion differences in phasing occurring in the northern extratropics are therefore not exclusively attributable to model biases. Model biases predominantly in the tropics contribute very likely to the most pronounced differences in the post-Pinatubo period (1991–1993) and the El Niño period (1997–1998), e.g., missing forcing to account for the effect of altered optical atmospheric thickness after the Pinatubo eruption [Roderick et al., 2001], and the anomalous C release to the atmosphere from biomass burning (2.1 ± 0.8 Pg C) in 1997–1998 [van der Werf et al., 2004], a process currently not considered in O-C.

[25] Figure 3b shows that the lower productivity simulated by O-CN relative to O-C between 50°N and 70°N, where the most notable difference occurs, is primarily due to (1) a lower simulated fraction of absorbed photosynthetically active radiation (FAPAR), caused by reduced foliage area per unit ground area; and (2) lower-foliage N concentrations. The poleward decline of FAPAR predicted by O-CN is more consistent with remotely sensed estimates from SeaWiFS [Gobron et al., 2006; Joint Research Center–Institute for Environment and Sustainability (JRC-IES), Earth Land Information System (ELIS): FAPAR, accessed 10 October 2008, available at <http://fapar.jrc.ec.europa.eu/Home.php>] than FAPAR estimates from O-C (Figure S4). However, comparisons with remotely sensed data are problematic and need to be interpreted with caution (see section 4 and Text S2). The foliage N content predicted by O-CN agrees well with the observed ranges (Figure S5) in the GLOPNET database [Wright et al., 2004]. There is a tendency toward high biased foliage N concentrations in dry regions with low simulated losses of N to leaching or emissions (see regions close to the tropics of cancer in Figure 3b). High-latitude tundra ecosystems equally show high foliar N concentrations in agreement with the observations by Wright et al. [2004], primarily as consequence of a colimitation of photosynthesis by temperature [McGuire et al., 1992]. Conversely, in boreal forest ecosystems with low rates of N deposition and biological N fixation, N concentrations in both broadleaved deciduous and evergreen needleleaved foliage tend to be at the low end of the observational range. Boreal ecosystems present the majority of the low biased foliage N concentrations simulated by O-CN.

3.3. Influence of the Terrestrial N Cycle on the Evolution of the Terrestrial C Balance, 1861–2002s

[26] Figure 5 summarizes the predicted global terrestrial C and N stocks and fluxes for the preindustrial and present-day (1990s mean) state; associated with historical changes in atmospheric [CO₂], climate, N deposition, and N fertilizer application. Both C and N cycling rates are predicted to have increased over time, with the terrestrial biosphere accumulating both organic C and N. In the 1990s, vegeta-

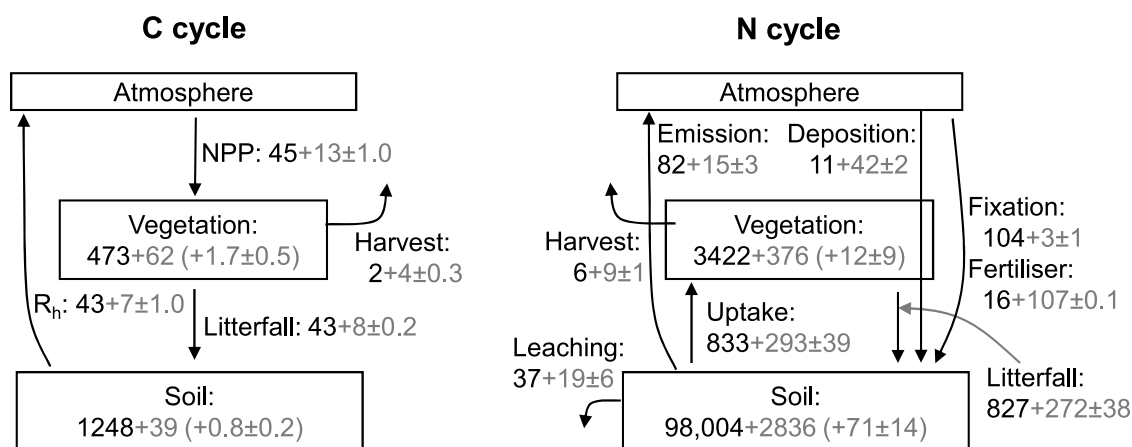


Figure 5. (left) Terrestrial carbon and (right) nitrogen cycles as simulated by O-CN, where black numbers denote preindustrial (1860s) values and gray numbers denote the changes that occurred because of historical changes in atmospheric $[\text{CO}_2]$, climate, N deposition, and N fertilizer application up to the 1990s. Vegetation and soil C and N stocks are given in Pg C and Tg N, respectively, and values in parentheses denote the respective annual rates of increase. All fluxes are given in Pg C yr^{-1} or Tg N yr^{-1} together with their decadal standard deviations.

tion sequestered C at a rate of $1.6 \pm 0.6 \text{ Pg C yr}^{-1}$ (decadal mean \pm standard deviation), requiring $12 \pm 10 \text{ Tg N yr}^{-1}$ (C:N of 133), whereas soil C stocks increased by $0.7 \pm 0.2 \text{ Pg C yr}^{-1}$, requiring $64 \pm 14 \text{ Tg N yr}^{-1}$ (C:N of 11). The total C and N imbalance in the 1990s is $2.4 \pm 0.6 \text{ Pg C yr}^{-1}$ and $76 \pm 14 \text{ Tg N yr}^{-1}$, signifying a terrestrial net storage. The estimate of global net C uptake is comparable to independent estimates of the residual terrestrial net C uptake such as is inferred from terrestrial net C uptake, minus net C losses due to land use changes, based on studies using observation and model-based approaches (1.6 to 4.8 Pg C yr^{-1}) [House *et al.*, 2003]. On the basis of models and observations, Galloway *et al.* [2004] estimated a present-day net N accumulation rate in the terrestrial biosphere of about 60 Tg N yr^{-1} . Cumulatively, vegetation contributed two thirds of the 111.3 Pg C sequestered globally between 1860 and 2002, but only around 15% of the 3.1 Pg N increment due to the wider C:N ratios of plant tissue than soil organic matter.

[27] The simulated imbalance of the terrestrial C flux, not accounting for any land use change related fluxes, has increased substantially since the 1960s (Figure S6). This net uptake is driven by a similar sized, gradually increasing C uptake in the northern extratropics and a substantially more variable uptake within the tropics. Southern extratropical regions contribute very little to the recent global net C uptake. Interestingly, the relative importance of the different drivers of the modern net C uptake in tropical and northern extratropics is substantially different (Figure 6). The simulated tropical net carbon uptake is almost entirely driven by increases in atmospheric $[\text{CO}_2]$ and associated increases in water use efficiency and productivity. This main effect is overlain by climatic variability and longer-term climatic changes causing strong decadal variation in the net C uptake, such that climate alone causes a net C source in the 1990s (Figure 6c). In contrast, northern

extratropical net C uptake is driven to a lesser extent by atmospheric $[\text{CO}_2]$ increases, with anthropogenic N deposition playing a stronger role. Concurrent changes in climate also contribute to the gradual increase in terrestrial C sequestration, due to both an increased growing season length and increasing N availability caused by accelerated soil organic matter decomposition in cold ecosystems.

[28] The spatial pattern of the net C uptake due to increasing N deposition follows the pattern of deposition and is thus strongest within between 35°N and 65°N (Figure 6d). Atmospheric deposition of reactive N over land has increased from about 11 Tg N yr^{-1} in the 1860s to about 53 Tg N yr^{-1} in the 1990s, with the highest loads being deposited in eastern North America, central Europe, India, and eastern China. In regions with large increases in N deposition, O-CN predicts minor increases in foliage N concentrations, foliage area, and annual productivity, mainly as consequences of reduced belowground allocation, consistent with site-scale observations [Elvira *et al.*, 2006]. In areas of high deposition, increased N availability increases annual net primary productivity by $\sim 20\%$, which is compatible with estimates from four process-based models [van Oijen *et al.*, 2008]. Since the 1860s, 65% of the anthropogenic additional reactive N input to the terrestrial biosphere from atmospheric deposition has accumulated in organic matter, with 25% lost to leaching and 10% lost to gaseous emissions (Figure S8). The largest losses occur in areas of high N deposition. About 85% ($\sim 900 \text{ Tg N}$) of the total additional reactive N retained in the terrestrial biosphere since the 1860s is stored in soil organic matter. Such partitioning was suggested earlier by Nadelhoffer *et al.* [1999] on the basis of tracer experiments. The 1990s mean global N imbalance resulting from N deposition alone is predicted to be 25 Tg N yr^{-1} , twice as large as the sequestration estimated recently by Schlesinger [2009] using a simple bookkeeping model.

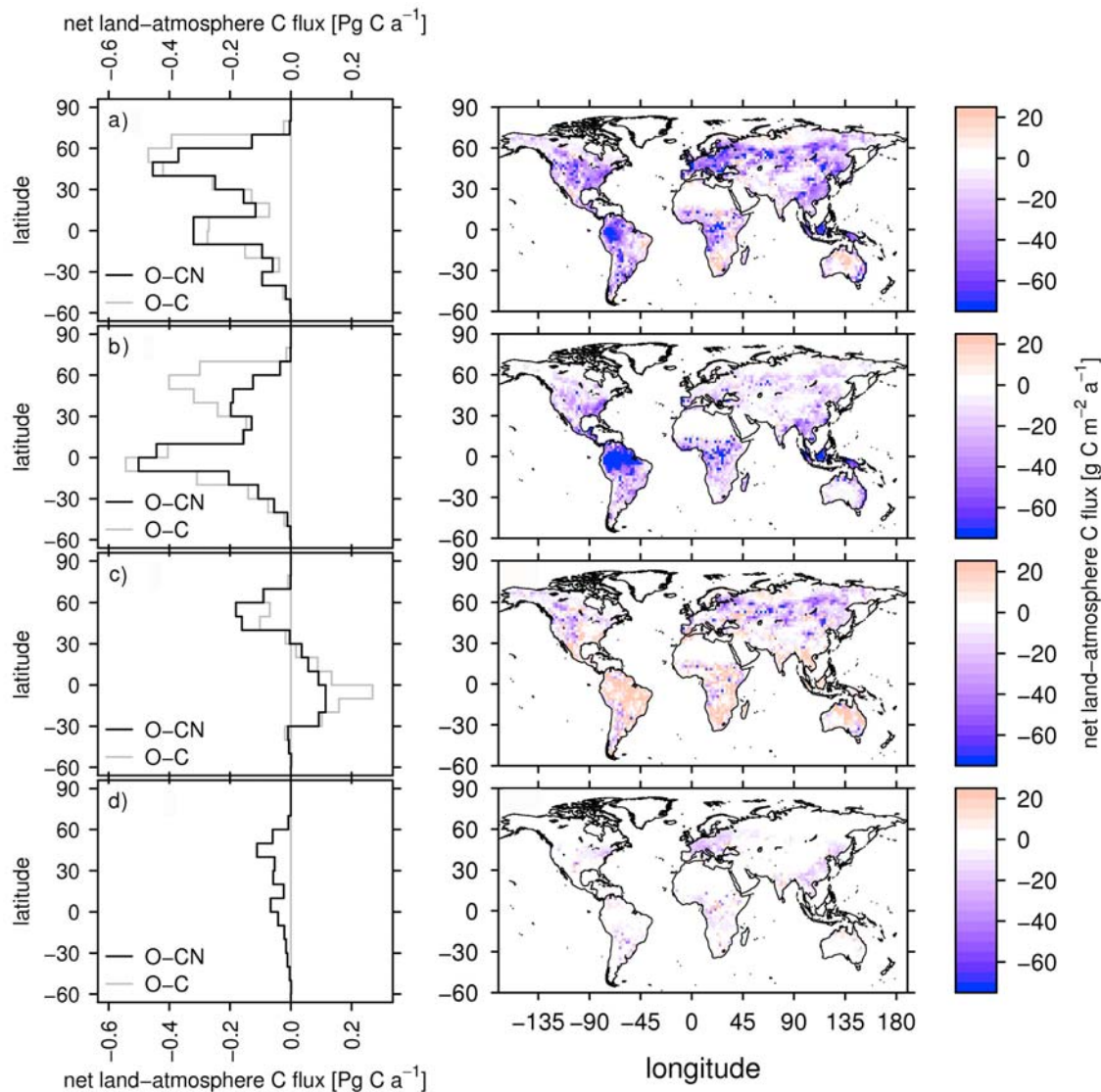


Figure 6. (left) Latitudinal distribution and (right) spatial patterns of the mean 1990s net land-atmosphere C flux: (a) resulting from the concurrent historical changes in atmospheric $[\text{CO}_2]$, climate, N deposition, and N fertilizer application; as well as split into the marginal contributions of (b) increases in atmospheric $[\text{CO}_2]$, (c) climatic changes, and (d) increases in N deposition. Results are based on the exclusion experiments (see Table 1). Spatial patterns are the net land-atmosphere C fluxes as simulated by O-CN.

[29] The arithmetic sum of the net C uptake in the 1990s due to the individual effects of atmospheric $[\text{CO}_2]$, climatic change, and N deposition is 1.7 Pg C yr^{-1} (sum of simulations S6, S7, and S8). The difference between this value and the net uptake of 2.1 Pg C yr^{-1} (simulation S2) resulting from the process-based combination of these three factors suggests a synergistic gain in the order of 0.4 Pg C yr^{-1} . The largest nonlinearities result from the interaction of atmospheric $[\text{CO}_2]$ with either N deposition or climatic changes, increasing net C uptake in both cases (Figure 7). The marginal effects of climate and N deposition on the marginal response to increasing atmospheric $[\text{CO}_2]$ are also positive and are of a comparable magnitude. There is no obvious pattern in the latitudinal distribution of these

interactions. The presence of these synergies precludes precise quantification of the effect of either factor on the present-day terrestrial net C balance. The net effect of N deposition is an increase of the net C uptake by $0.2\text{--}0.5 \text{ Pg C yr}^{-1}$, corresponding to 8–20% of the simulated net C uptake during the 1990s. Increasing atmospheric $[\text{CO}_2]$ remains the major cause for the simulated net C uptake, despite a reduction of its influence due to the N cycle constraint of 0.9 Pg C yr^{-1} , accounting for the synergistic effects of covarying factors.

[30] Explicitly accounting for N dynamics reduces high-latitude ($>50^\circ\text{N}$) net C uptake by 0.4 Pg C yr^{-1} in O-CN compared to O-C (Figure 6a). This is mainly a consequence of N limitation causing a much weaker response of plant

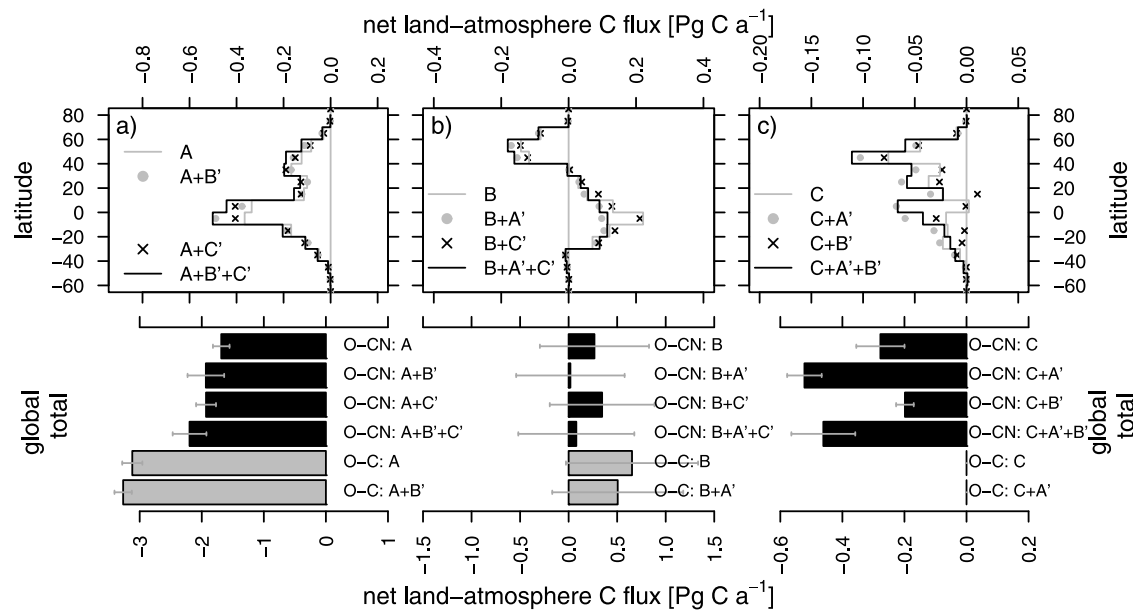


Figure 7. (top) Latitudinal distribution and (bottom) global total of the marginal contributions of (a) increased atmospheric $[\text{CO}_2]$ (contribution A), (b) climatic changes (contribution B), and (c) N deposition (contribution C) on the 1990s average net land-atmosphere C exchange. Plotted are the single factor contributions (denoted as contributions A, B, or C) and the marginal synergistic (or antagonistic) effects of covarying factors (denoted as contributions A', B', or C').

growth to increasing atmospheric $[\text{CO}_2]$ (Figure 6b). The reduction is not compensated for by the effects of concurrent climatic changes and increased N deposition, both of which enhance high-latitude N availability and net C uptake (Figures 6c–6d). This is true despite O-CN's stronger high-latitude net C uptake in response to climatic change. While both O-C and O-CN account for the effect of an increasing growing season length on vegetation growth, the increase in productivity and net C uptake in O-CN is further enhanced by the stimulating effect of enhanced soil organic matter decomposition and thus net N mineralization. The response of the tropical net C uptake in O-CN to increases in atmospheric $[\text{CO}_2]$ and climatic changes appears to be slightly dampened relative to O-C; however, the magnitude and distribution of the resulting present-day net C uptake are very similar between the two model versions. Accounting for N dynamics increases the magnitude of synergistic effects between individual model forcings on net land-atmosphere exchange (Figure 7).

4. Discussion

4.1. Evaluation of the Model Performance

[31] This paper presents a comprehensive assessment of the new carbon and nitrogen parameterizations incorporated into the land surface scheme ORCHIDEE. Zaehle and Friend [2010] assessed the performance of O-CN using in situ observations and found that the model simulates well the observed vegetation productivity at a wide range of European temperate and boreal sites. This analysis has been extended here to the global scale by comparison with a global database of vegetation productivity and has demon-

strated satisfactory agreement across various vegetation types. Such an analysis is not without difficulties due to geographic sampling biases that often exclude remote areas. The estimates of the database by *Luysaert et al.* [2007], for instance, contain precise measurements of productivity at the local scale, but may not necessarily be representative of biome-scale vegetation productivity because of an under-sampling of geographically remote regions, evidenced as difference between simulated site-level and global estimates (Table S3).

[32] Remotely sensed observations of the annual maximum fraction of absorbed photosynthetically active radiation (FAPAR) provide estimates of geographic variation in annual maximum foliage area, a key component of the N cycle constraint on plant growth. The use of annual maximum FAPAR as a model evaluation data also facilitates the comparison with remote-sensing products by obviating confounding effects of changing spectral properties during the growing season [*Gobron et al.*, 2006]. However, inconsistencies due to different assumptions concerning canopy light extinction and reflection, and confounding effects due to subpixel heterogeneity and sparse versus closed canopies, cannot be completely excluded (see also discussion by *Tian et al.* [2004]), and may contribute to biases when comparing remotely sensed and simulated FAPAR values for equivalent land cover types. This cautions against an overly quantitative interpretation of comparisons between simulated and remotely sensed FAPAR values. Despite these concerns, there is little evidence that the increasing difference in FAPAR between O-CN and O-C along the Northern Hemispheric south to north transects results from a systematic underestimation of foliage projected area by O-CN.

Rather, there is an improvement in the simulated poleward decline of FAPAR in O-CN in comparison with O-C.

[33] The evaluation of the simulated seasonal cycle of atmospheric $[\text{CO}_2]$ at monitoring stations is subject to uncertainty from atmospheric transport modeling, which can result in differences in the peak to peak amplitude of up to 10 ppm at high northern latitude stations between different transport models [Law *et al.*, 1996]. Bousquet *et al.* [2008] have shown that the LMDz model used in this study has a slight tendency to produce a shallower seasonal cycle at the high-latitude stations than regional transport models. This could have contributed to the underestimation of the amplitude of the seasonal cycle in O-CN both at mid and high latitude sites (Figure 2). However, this explanation is probably not sufficient to account for the underestimation by O-CN at all high-latitude monitoring stations; a view supported by the comparison to the inversion-based mean seasonal cycle (Figure S3) by Baker *et al.* [2006].

[34] Processes controlling the seasonality of the carbon cycle other than those affected by the terrestrial N cycle, such as the temperature responses of photosynthesis or soil organic matter decomposition, the parameterization of soil hydrology, or the surface energy balance, could contribute to this underestimation. However, the low bias in the simulated boreal foliage N concentrations supports the idea that O-CN's terrestrial high-latitude summer C uptake low bias is due to a too strong N constraint on plant growth in the boreal zone, despite the good agreement with the GPP and NPP observations. Potential reasons for this are the lack of a representation of one or more of the following processes: (1) ecosystem disturbances such as fire or insect outbreaks causing mineralization of N locked up in organic matter [Smithwick *et al.*, 2005]; (2) direct uptake of organic N, bypassing the mineralization pathway of organic material [Jones *et al.*, 2005]; or (3) underestimation of biological N fixation rates in boreal and Arctic ecosystems.

[35] Although global C and N cycling compares preferably to independent global estimates, there are some regional biases: Tropical C:N ratios are on average, but not generally, higher than observed [Vitousek *et al.*, 1988; Williams *et al.*, 2002]. This is likely a consequence of an observation-based estimate of biological N fixation which implicitly accounts for phosphorous (P) availability, whereas P availability is not taken into account for the simulation of C uptake through photosynthesis. However, the slightly higher C:N does not strongly affect tropical NPP (Figure 3), the seasonal cycle of the land-atmosphere flux in the tropics (Figure 2c), or the present-day net C uptake (Figure 6a). This bias is therefore likely to be of minor importance for the simulated global C cycling, but contributes to the low estimate of tropical N_2O emissions (results not shown).

[36] Modeled boreal soil C stocks are within the range of reported values from soil profiles [Ping *et al.*, 2008], but the total soil C in the boreal zone is biased low relative to a recent extrapolation of site measurements [Ping *et al.*, 2008]. This is likely due to the lack of representing the slowing effect of soil water saturation and freezing on decomposition in permafrost and wetland soils. Whether or not this bias will significantly influence future C cycle projections is still a matter of debate [Schuur *et al.*, 2009]. A

future version of O-CN will incorporate these dependencies to address the likely consequences of this bias.

[37] Our understanding of global terrestrial N stocks and fluxes is much less advanced in comparison with the global carbon cycle [Gruber and Galloway, 2008] because of (1) the rapid turnover of reactive N in terrestrial ecosystems, rendering it difficult to observe the desired quantities (e.g., net mineralization rates); (2) technical challenges in observing the complete N budget at the site scale; (3) the scarcity of suitable observations on reactive trace gas and leaching losses to scale these up to regional and global estimates [Boyer *et al.*, 2006a]; and (4) the vast reserve of atmospheric N_2 swamping any atmospheric terrestrial signal. As such, the comparisons of the reactive N fluxes presented in this paper serve as a general verification of the magnitudes of the simulated fluxes rather than a quantitative model evaluation. Future work will focus on increasing the constraints on these fluxes through the use of site-scale measurements [Sutton *et al.*, 2007]. Three key areas that need to be addressed are (1) the controls by soil moisture and soil hydrology on denitrification rates and the loss rate of any gaseous species to the atmosphere, which affect the partitioning between individual N species [Del Grosso *et al.*, 2005]; (2) the interactions of reactive N species, namely NO_x , with the canopy [Ganzeveld *et al.*, 2002]; and (3) the representation of crop management and fertilizer application [Stehfest, 2005].

[38] While the above discussion shows that further work on individual processes will still be necessary, the results presented here demonstrate the generally satisfactory degree to which O-CN is capable of simulating the contemporary C and N cycles. Although the skill of a complex ecosystem model such as ours is necessarily a qualitative judgement depending on the vagaries of observational data and the intended applications, we believe that O-CN provides an adequate enough representation of terrestrial N cycling and its constraint on terrestrial C cycling to study the effect of N cycling on the global C cycle. Because of this capacity, O-CN provides a major improvement over the model version not explicitly accounting for N dynamics. The skill of the model to simulate the effect of N dynamics on terrestrial responses to future atmospheric $[\text{CO}_2]$, warming, and increased N inputs will be evaluated in a forthcoming paper.

4.2. Effects of Accounting for the N Cycle Constraint on Simulations of the Global C Balance

[39] The contemporary simulated global C cycles of both O-C and O-CN are commensurate with our current understanding of the C cycle. The cumulative net C uptake over the simulation period, 130 and 111 Pg C in O-C and O-CN, respectively, differ by 19 Pg C or 15%. It is unlikely that the observed historical atmospheric $[\text{CO}_2]$ record would provide a sufficiently strong constraint to distinguish between the two model versions using a complete carbon cycle model [Friedlingstein *et al.*, 2006]. However, the 0.4 Pg C yr^{-1} smaller high-latitude net C uptake in O-CN is closer to the relatively low rates of high latitude C uptake calculated by a recent inversion study [Stephens *et al.*, 2007]. Although the 1990s average global net C uptake does not differ strongly between the two model versions, the driving factors of terrestrial C dynamics do, changing the

sensitivity of the terrestrial biosphere to both climate and atmospheric $[\text{CO}_2]$ forcings. Accounting for N dynamics leads to a higher degree of interaction between individual model forcings by increasing the coupling between vegetation and soil process. However, it is not clear whether this higher degree of interaction stabilizes the terrestrial C balance with respect to its response to future environmental changes, as has been suggested by recent modeling studies [Thornton *et al.*, 2007; Sokolov *et al.*, 2008]. The differences between O-C and O-CN will likely have substantial consequences for projections of the terrestrial carbon balance into the future, such as performed by Cramer *et al.* [2001] and Friedlingstein *et al.* [2006], as demonstrated by Zaehle *et al.* [2010].

[40] Notwithstanding the N cycle constraint, the increase in atmospheric $[\text{CO}_2]$ remains the dominant cause of the recent simulated net terrestrial C uptake. N deposition contributes about 8–20% (0.2–0.52 Pg C yr⁻¹) of O-CN's predicted terrestrial net C uptake, with the lower estimate being closer to the “true” N effect, i.e., considered N deposition in isolation from concurrent changes in other forcings. The responsiveness of terrestrial C sequestration to N deposition is in the order of 40 g C g⁻¹ N and thus comparable to that estimated from isotopic tracer studies [Nadelhoffer *et al.*, 1999], forest monitoring plots [De Vries *et al.*, 2006], and fertilizer studies [Hyvonen *et al.*, 2007]. As discussed by Zaehle and Friend [2010], the response is much smaller than initially suggested by Magnani *et al.* [2007] based on eddy-covariance data. The simulated latitudinal distribution of net terrestrial C uptake follows that of N deposition, as suggested by Townsend *et al.* [1996] based on stoichiometric considerations. The global magnitude of the marginal C uptake due to N deposition simulated with O-CN is comparable to estimates based on extrapolation of isotopic tracer experiments in temperate forests (i.e., 0.25 Pg C yr⁻¹, Nadelhoffer *et al.* [1999]), a simple stoichiometric C growth model driven by modern N deposition fields (i.e., 0.4–0.7 Pg C yr⁻¹, Townsend *et al.* [1996]), and results of the process-based model CLM-CN (i.e., 0.24 Pg C yr⁻¹, Thornton *et al.* [2007]).

[41] Taking account of land management and historical changes in land use will further influence the simulated net land-atmosphere C flux [House *et al.*, 2003] and will thus need to be accounted for in future studies. O-CN predicts that cropland soils took up about 0.4 Pg C yr⁻¹ in the 1990s, mainly due to increases in productivity caused by the application of industrial fertilizer and increased N deposition from a low preindustrial level. Changes in cropland extent and management, such as tillage intensity and the amount of residual organic matter removed from the site during harvest, which affect soil organic matter stocks and their dynamics [Guo and Gifford, 2002], were not taken into account. Historical change in land use would further affect the results by decreasing the net tropical C uptake due to deforestation C losses [House *et al.*, 2003], and likely increasing temperate C sequestration due to the combined effects of reforestation and forest management [Zaehle *et al.*, 2006]. However, taking account of land use changes would not affect any of our conclusions related to the

general importance of N cycling for the estimation of terrestrial productivity or the net C balance.

5. Concluding Remarks

[42] The results presented here show that the coupling of the terrestrial carbon and nitrogen cycles in O-CN results in realistic overall global patterns of carbon and nitrogen fluxes despite some regional biases. The new model compares favorably with benchmarks of local productivity, the observational record of atmospheric CO_2 concentrations, and a literature compilation of terrestrial C and N stocks, concentrations, and fluxes.

[43] Using this new model to estimate the present-day terrestrial C balance leads to three main conclusions:

[44] 1. Terrestrial biosphere models that omit N limitations likely overestimate high-latitude C sequestration due to climate change and increasing atmospheric $[\text{CO}_2]$. Our results suggest that this overestimation could be about 0.4 Pg C yr⁻¹.

[45] 2. The effect of N deposition on global C sequestration, although locally important, explains less than 20% of the recent global terrestrial net C uptake related to changes in atmospheric composition and climate. While this may not seem much, it is of a scale relevant to current efforts to reduce anthropogenic CO_2 emissions.

[46] 3. Accounting for N cycle constraints on terrestrial C dynamics fundamentally alters the relative importance of the processes driving those dynamics, with very likely major impacts on projections of future global terrestrial C balance and its distribution.

[47] **Acknowledgments.** The authors are very grateful to V. Prieur and N. Viovy for discussions of the modeling concept, to N. Gobron and M. Jung for help with the JRC FAPAR product derived from SeaWiFS (NASA), and to two anonymous reviewers for constructive comments on earlier versions of this manuscript. Funding from the Marie-Curie Research and Training Network GREENCYCLES (MRTN-CT-2004-512464) and the Marie Curie European Reintegration grant JULIA (PERG02-GA-2007-224775) is also gratefully acknowledged. Computer time was supplied by the Centre d'Énergie Atomique (CEA).

References

- Anderson, J. (1973), The breakdown and decomposition of sweet chestnut (*Castanea sativa* Mill.) and beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodland soils: II. Changes in the carbon, nitrogen and polyphenol content, *Oecologia*, 12, 275–288.
- Baker, D. F., et al. (2006), TransCom 3 inversion intercomparison: Impact of transport model errors on the interannual variability of regional CO_2 fluxes, 1988–2003, *Global Biogeochem. Cycles*, 20, GB1002, doi:10.1029/2004GB002439.
- Bousquet, P., F. Delage, C. Carouge, L. Klenov, C. Aulagnier, M. Ramonet, and F. Chevallier (2008), *Evaluation of the LMDz model for the representation of the atmospheric CO_2 concentrations*, 42 pp., EU-project GEMS, Eur. Cent. for Medium-Range Weather Forecasts, Reading, U. K. (Available at <http://gems.ccmwf.int/do/get/PublicDocuments/1529/770>)
- Boyer, E. W., R. B. Alexander, W. J. Parton, C. S. Li, K. Butterbach-Bahl, S. D. Donner, R. W. Skaggs, and S. J. Del Gross (2006a), Modeling denitrification in terrestrial and aquatic ecosystems at regional scales, *Ecol. Appl.*, 16, 2123–2142, doi:10.1890/1051-0761(2006)016[2123:MDITAA]2.0.CO;2.
- Boyer, E. W., R. W. Howarth, J. N. Galloway, F. J. Dentener, P. A. Green, and C. J. Vorosmarty (2006b), Riverine nitrogen export from the continents to the coasts, *Global Biogeochem. Cycles*, 20, GB1S91, doi:10.1029/2005GB002537.

- Ciais, P., et al. (1997), A three-dimensional synthesis study of delta O-18 in atmospheric CO₂: 1. Surface fluxes, *J. Geophys. Res.*, *102*, 5857–5872, doi:10.1029/96JD02360.
- Cramer, W., et al. (2001), Global response of terrestrial ecosystem structure and function to CO₂ and climate change: Results from six dynamic global vegetation models, *Global Change Biol.*, *7*, 357–373, doi:10.1046/j.1365-2486.2001.00383.x.
- Davidson, E. A., and W. Kingerlee (1997), A global inventory of nitric oxide emissions from soils, *Nutr. Cycl. Agroecosyst.*, *48*, 37–50, doi:10.1023/A:1009738715891.
- Del Grosso, S. J., A. R. Mosier, W. J. Parton, and D. S. Ojima (2005), DAYCENT model analysis of past and contemporary soil N₂O and net greenhouse gas flux for major crops in the USA, *Soil Tillage Res.*, *83*, 9–24, doi:10.1016/j.still.2005.02.007.
- Denman, K. L., et al. (2007), Couplings between changes in the climate system and biogeochemistry, in *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by S. Solomon et al., pp. 511–539, Cambridge Univ. Press, Cambridge, U. K.
- De Vries, W., G. J. Reinds, P. Gundersen, and H. Sterba (2006), The impact of nitrogen deposition on carbon sequestration in European forests and forest soils, *Global Change Biol.*, *12*, 1151–1173, doi:10.1111/j.1365-2486.2006.01151.x.
- Ducoudré, N. I., K. Laval, and A. Perrier (1993), SECHIBA, a new set of parameterizations of the hydrologic exchanges at the land-atmosphere interface within the LMD atmospheric general circulation model, *J. Clim.*, *6*, 248–273, doi:10.1175/1520-0442(1993)006<0248:SANSOP>2.0.CO;2.
- Elvira, J. A., G. B. Wiersmab, M. E. Dayc, M. S. Greenwoodd, and I. J. Fernandez (2006), Effects of enhanced nitrogen deposition on foliar chemistry and physiological processes of forest trees at the Bear Brook Watershed in Maine, *For. Ecol. Manage.*, *22*, 207–214.
- Field, C. B., and H. Mooney (1986), The photosynthesis-nitrogen relationship in wild plants, in *On the Economy of Plant Form and Function*, edited by T. Givinish, pp. 25–55, Cambridge Univ. Press, Cambridge, U. K.
- Flanagan, P., and K. van Cleve (1983), Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems, *Can. J. For. Res.*, *13*, 795–817, doi:10.1139/x83-110.
- Friedlingstein, P., G. Joel, C. B. Field, and I. Y. Fung (1999), Toward an allocation scheme for global terrestrial carbon models, *Global Change Biol.*, *5*, 755–770, doi:10.1046/j.1365-2486.1999.00269.x.
- Friedlingstein, P., et al. (2006), Climate-carbon cycle feedback analysis: Results from the C⁴MIP model intercomparison, *J. Clim.*, *19*, 3337–3353, doi:10.1175/JCLI3800.1.
- Friend, A. D., and N. Y. Kiang (2005), Land-surface model development for the GISS GCM: Effects of improved canopy physiology on simulated climate, *J. Clim.*, *18*, 2883–2902, doi:10.1175/JCLI3425.1.
- Friend, A. D., A. K. Stevens, R. G. Knox, and M. G. R. Cannell (1997), A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0), *Ecol. Modell.*, *95*, 249–287, doi:10.1016/S0304-3800(96)00034-8.
- Galloway, J. N., et al. (2004), Nitrogen cycles: Past, present and future, *Biogeochemistry*, *70*, 153–226, doi:10.1007/s10533-004-0370-0.
- Ganzeveld, L. N., J. Lelieveld, F. J. Dentener, M. C. Krol, A. J. Bouwman, and G. J. Roelofs (2002), Global soil-biogenic NO_x emissions and the role of canopy processes, *J. Geophys. Res.*, *107*(D16), 4298, doi:10.1029/2001JD001289.
- GLOBALVIEW-CO₂ (2007), *Cooperative Atmospheric Data Integration Project—Carbon Dioxide* [CD-ROM], CMDL, NOAA, Boulder, Colo.
- Gobron, N., et al. (2006), Evaluation FAPAR products for different canopy radiation transfer regimes: Methodology and results using JRC products derived from SeaWiFS against ground-based estimations, *J. Geophys. Res.*, *111*, D13110, doi:10.1029/2005JD006511.
- Gruber, N., and J. N. Galloway (2008), An Earth-system perspective of the global nitrogen cycle, *Nature*, *451*, 293–296, doi:10.1038/nature06592.
- Guo, L. B., and R. M. Gifford (2002), Soil carbon stocks and land use change: A meta analysis, *Global Change Biol.*, *8*, 345–360, doi:10.1046/j.1354-1013.2002.00486.x.
- Heimann, M., et al. (1998), Evaluation of terrestrial carbon cycle models through simulations of the seasonal cycle of atmospheric CO₂: First results of a model intercomparison study, *Global Biogeochem. Cycles*, *12*, 1–24, doi:10.1029/97GB01936.
- Hirsch, A. I., A. M. Michalak, L. M. Bruhwiler, W. Peters, E. J. Dlugokencky, and P. P. Tans (2006), Inverse modeling estimates of the global nitrous oxide surface flux from 1998–2001, *Global Biogeochem. Cycles*, *20*, GB1008, doi:10.1029/2004GB002443.
- Houlton, B. Z., Y. P. Wang, P. M. Vitousek, and C. B. Field (2008), A unifying framework for dinitrogen fixation in the terrestrial biosphere, *Nature*, *454*, 327–330, doi:10.1038/nature07028.
- House, J. I., I. C. Prentice, N. Ramankutty, R. A. Houghton, and M. Heimann (2003), Reconciling apparent inconsistencies in estimates of terrestrial CO₂ sources and sinks, *Tellus, Ser. B*, *55*, 345–363, doi:10.1034/j.1600-0889.2003.00037.x.
- Hungate, B. A., J. S. Dukes, M. R. Shaw, Y. Luo, and C. B. Field (2003), Nitrogen and climate change, *Science*, *302*, 1512–1513, doi:10.1126/science.1091390.
- Hyvonen, R., et al. (2007), The likely impact of elevated [CO₂], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: A literature review, *New Phytol.*, *173*, 463–480, doi:10.1111/j.1469-8137.2007.01967.x.
- Jones, D. L., J. R. Healey, V. B. Willett, J. F. Farrar, and A. Hodge (2005), Dissolved organic nitrogen uptake by plants—an important N uptake pathway?, *Soil Biol. Biochem.*, *37*, 413–423, doi:10.1016/j.soilbio.2004.08.008.
- Kirschbaum, M. U. F., and K. I. Paul (2002), Modelling C and N dynamics in forest soils with a modified version of the CENTURY model, *Soil Biol. Biochem.*, *34*, 341–354, doi:10.1016/S0038-0717(01)00189-4.
- Knorr, W., and M. Heimann (1995), Impact of drought stress and other factors on seasonal land biosphere CO₂ exchange studied through an atmospheric tracer transport model, *Tellus, Ser. B*, *47*, 471–489, doi:10.1034/j.1600-0889.47.issue4.7.x.
- Krinner, G., N. Viovy, N. de Noblet-Ducoudré, J. Ogée, J. Polcher, P. Friedlingstein, P. Ciais, S. Sitch, and I. C. Prentice (2005), A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system, *Global Biogeochem. Cycles*, *19*, GB1015, doi:10.1029/2003GB002199.
- Law, R. M., et al. (1996), Variations in modelled atmospheric transport of carbon dioxide and the consequences for CO₂ inversions, *Global Biogeochem. Cycles*, *10*, 783–796, doi:10.1029/96GB01892.
- Li, C. S., J. Aber, F. Stange, K. Butterbach-Bahl, and H. Papen (2000), A process-oriented model of N₂O and NO emissions from forest soils: 1. Model development, *J. Geophys. Res.*, *105*, 4369–4384, doi:10.1029/1999JD900949.
- Luo, Y., et al. (2004), Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide, *BioScience*, *54*, 731–739, doi:10.1641/0006-3568(2004)054[0731:PNLOER]2.0.CO;2.
- Luo, Y. Q., C. B. Field, and R. B. Jackson (2006), Does nitrogen constrain carbon cycling, or does carbon input stimulate nitrogen cycling?, *Ecology*, *87*, 3–4, doi:10.1890/05-0923.
- Luyssaert, S., et al. (2007), CO₂ balance of boreal, temperate, and tropical forests derived from a global database, *Global Change Biol.*, *13*, 2509–2537, doi:10.1111/j.1365-2486.2007.01439.x.
- Magnani, F., et al. (2007), The human footprint in the carbon cycle of temperate and boreal forests, *Nature*, *447*, 849–851, doi:10.1038/nature05847.
- Marti, O., et al. (2005), *The New IPSL Climate System Model: IPSL-CM4*, 84 pp., IPSL, Paris.
- McGuire, A., J. Melillo, L. Joyce, D. Kicklighter, A. Grace, I. B. Moore, and C. 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, doi:10.1029/92GB00219.
- Melillo, J. M., A. D. McGuire, D. W. Kicklighter, B. Moore, C. J. Vorosmarty, and A. L. Schloss (1993), Global climate change and terrestrial net primary production, *Nature*, *363*, 234–240, doi:10.1038/363234a0.
- Melillo, J. M., et al. (2002), Soil warming and carbon cycle feedbacks to the climate system, *Science*, *298*, 2173–2176, doi:10.1126/science.1074153.
- Mitchell, T. D., T. R. Carter, P. D. Jones, M. Hulme, and M. New (2004), *A Comprehensive Set of High-Resolution Grids of Monthly Climate for Europe and the Globe: The Observed Record (1901–2000) and 16 Scenarios (2001–2100)*, 33 pp., Tyndall Cent. for Clim. Change Res., Univ. of East Anglia, Norwich, U. K.
- Nadelhoffer, K., B. Emmet, P. Gundersen, O. Kjonaas, C. Koopmans, P. Schlegli, A. Tietma, and R. Wright (1999), Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests, *Nature*, *398*, 145–148, doi:10.1038/18205.
- Olivier, J. G. J., A. F. Bouwman, K. W. Van der Hoek, and J. J. M. Berdowski (1998), Global air emission inventories for anthropogenic sources of NO_x, NH₃ and N₂O in 1990, *Environ. Pollut.*, *102*, 135–148, doi:10.1016/S0269-7491(98)80026-2.
- Parton, W. J., et al. (1993), Observations and modelling of biomass and soil organic matter dynamics for the grassland biome worldwide, *Global Biogeochem. Cycles*, *7*, 785–809, doi:10.1029/93GB02042.

- Peylin, P., P. Bousquet, C. Le Quéré, S. Sitch, P. Friedlingstein, G. McKinley, N. Gruber, P. Rayner, and P. Ciais (2005), Multiple constraints on regional CO₂ flux variations over land and oceans, *Global Biogeochem. Cycles*, *19*, GB1011, doi:10.1029/2003GB002214.
- Ping, C.-L., G. J. Michaelson, M. T. Jorgenson, J. M. Kimble, H. Epstein, V. E. Romanovsky, and D. A. Walker (2008), High stocks of soil organic carbon in the North American Arctic region, *Nat. Geosci.*, *1*, 615–619, doi:10.1038/ngeo284.
- Post, W. M., W. R. Emanuel, P. J. Zinke, and A. G. Stangenberger (1982), Soil carbon pools and world life zones, *Nature*, *298*, 156–159, doi:10.1038/298156a0.
- Post, W. M., J. Pastor, P. J. Zinke, and A. G. Stangenberger (1985), Global patterns of soil nitrogen storage, *Nature*, *317*, 613–616, doi:10.1038/317613a0.
- Prentice, I. C., M. Heimann, and S. Sitch (2000), The carbon balance of the terrestrial biosphere: Ecosystem models and atmospheric observations, *Ecol. Appl.*, *10*, 1553–1573, doi:10.1890/1051-0761(2000)010[1553:TCBOTT]2.0.CO;2.
- Prentice, I. C., et al. (2001), The carbon cycle and atmospheric carbon dioxide, in *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*, edited by J. T. Houghton et al., Cambridge Univ. Press, Cambridge, U. K.
- Roderick, M. L., G. D. Farquhar, S. L. Berry, and I. R. Noble (2001), On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation, *Oecologia*, *129*, 21–30, doi:10.1007/s004420100760.
- Saugier, B., and J. Roy (2001), Estimations of global terrestrial productivity: Converging towards a single number?, in *Global Terrestrial Productivity: Past, Present and Future*, edited by H. Mooney, J. Roy, and B. Saugier, Academic, San Diego, Calif.
- Schlesinger, W. H. (1991), *Biogeochemistry: An Analysis of Global Change*, Academic, San Diego, Calif.
- Schlesinger, W. H. (2009), On the fate of anthropogenic nitrogen, *Proc. Natl. Acad. Sci. U. S. A.*, *106*, 203–208, doi:10.1073/pnas.0810193105.
- Schuur, E. A. G., J. G. Vogel, K. G. Crummer, H. Lee, J. O. Sickman, and T. E. Osterkamp (2009), The effect of permafrost thaw on old carbon release and net carbon exchange from tundra, *Nature*, *459*, 556–559, doi:10.1038/nature08031.
- Shinozaki, K., K. Yoda, K. Hozumi, and T. Kira (1964), A quantitative analysis of the plant form: The pipe model theory, *Jpn. J. Ecol.*, *14*, 98–104.
- Sitch, S., et al. (2003), Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model, *Global Change Biol.*, *9*, 161–185, doi:10.1046/j.1365-2486.2003.00569.x.
- Smithwick, E. A. H., M. G. Turner, M. C. Mack, and F. S. Chapin III (2005), Post-fire soil N cycling in northern conifer forests affected by severe stand-replacing wildfires, *Ecosystems*, *8*, 163–181, doi:10.1007/s10021-004-0097-8.
- Sokolov, A. P., D. W. Kicklighter, J. M. Melillo, B. S. Felzer, C. A. Schlosser, and T. W. Cronin (2008), Consequences of considering carbon-nitrogen interactions on the feedbacks between climate and the terrestrial carbon cycle, *J. Clim.*, *21*, 3776–3796, doi:10.1175/2008JCLI2038.1.
- Sprugel, D. G., M. G. Ryan, J. R. Brooks, K. A. Vogt, and T. A. Martin (1996), Respiration from the organ level to the stand, in *Resource Physiology of Conifers*, edited by K. Smith and T. M. Hinckley, pp. 255–299, Academic, San Diego, Calif.
- Stehfest, E. (2005), *Modelling of Global Crop Production and Resulting N₂O Emissions*, 167 pp., Cent. for Environ. Syst. Res., Int. Max Planck Res. School on Earth Syst. Modell., Univ. Kassel, Kassel, Germany.
- Stehfest, E., and L. Bouwman (2006), N₂O and NO emission from agricultural fields and soils under natural vegetation: Summarizing available measurement data and modeling of global annual emissions, *Nutr. Cycl. Agroecosyst.*, *74*, 207–228, doi:10.1007/s10705-006-9000-7.
- Stephens, B. B., et al. (2007), Weak northern and strong tropical land carbon uptake from vertical profiles of atmospheric CO₂, *Science*, *316*, 1732–1735, doi:10.1126/science.1137004.
- Sutton, M. A., et al. (2007), Challenges in quantifying biosphere-atmosphere exchange of nitrogen species, *Environ. Pollut.*, *150*, 125–139, doi:10.1016/j.envpol.2007.04.014.
- Sutton, M. A., D. Simpson, P. E. Levy, R. I. Smith, S. Reis, M. van Oijen, and W. De Vries (2008), Uncertainties in the relationship between atmospheric nitrogen deposition and forest carbon sequestration, *Global Change Biol.*, *14*, 2057–2063, doi:10.1111/j.1365-2486.2008.01636.x.
- Thornton, P. E., J. F. Lamarque, N. A. Rosenbloom, and N. M. Mahowald (2007), Inclusion of carbon-nitrogen cycle coupling on land model response to CO₂ fertilization and climate variability, *Global Biogeochem. Cycles*, *21*, GB4018, doi:10.1029/2006GB002868.
- Tian, Y., et al. (2004), Comparison of seasonal and spatial variations of leaf area index and fraction of absorbed photosynthetically active radiation from Moderate Resolution Imaging Spectroradiometer (MODIS) and Common Land Model, *J. Geophys. Res.*, *109*, D01103, doi:10.1029/2003JD003777.
- Townsend, A., B. H. Braswell, E. Holland, and J. Penner (1996), Spatial and temporal patterns in potential terrestrial carbon storage due to deposition of fossil fuel derived nitrogen, *Ecol. Appl.*, *6*, 806–814, doi:10.2307/2269486.
- van der Werf, G. R., J. T. Randerson, G. J. Collatz, L. Giglio, P. S. Kasibhatla, A. F. Arellano Jr., S. C. Olsen, and E. S. Kasischke (2004), Continental-scale partitioning of fire emissions during the 1997 to 2001 El Niño/La Niña period, *Science*, *303*, 73–76, doi:10.1126/science.1090753.
- van Oijen, M., and P. Levy (2004), Nitrogen metabolism and plant adaptation to the environment: The scope for process-based modeling, in *Nitrogen Acquisition and Assimilation in Higher Plants*, *Plant Ecophysiol. Ser.*, vol. 3, edited by S. Amâncio and I. Stulen, pp. 133–147, Kluwer Acad., Dordrecht, Netherlands.
- van Oijen, M., G. I. Agren, O. Chertov, S. Kellomaki, A. Komarov, D. Mobbs, and M. Murray (2008), Evaluation of past and future changes in European forest growth by means of four process-based models, in *Causes and Consequences of Forest Growth Trends in Europe*, *EFI Res. Rep.*, vol. 21, edited by H. P. Kahle et al., chap. 4.4, pp. 183–199, Brill Publ., Leiden, Netherlands.
- Viovy, N. (1996), Interannuality and CO₂ sensitivity of the SECHIBA-BGC coupled SVAT-BGC model, *Phys. Chem. Earth*, *21*, 489–497, doi:10.1016/S0079-1946(97)81147-0.
- Vitousek, P. M., and R. W. Howarth (1991), Nitrogen limitation on land and in the sea: How it can occur, *Biogeochemistry*, *13*, 87–115, doi:10.1007/BF00002772.
- Vitousek, P. M., T. Fahey, D. W. Johnson, and M. J. Swift (1988), Element interactions in forest ecosystems: Succession, allometry and input-output budgets, *Biogeochemistry*, *5*, 7–34, doi:10.1007/BF02180316.
- Williams, M., Y. E. Shimabukuro, D. A. Herbert, S. P. Lacruz, C. Renno, and E. B. Rastetter (2002), Heterogeneity of soils and vegetation in an eastern Amazonian rain forest: Implications for scaling up biomass and production, *Ecosystems*, *5*, 692–704, doi:10.1007/s10021-002-0165-x.
- Woodward, F. I., T. M. Smith, and W. R. Emanuel (1995), A global land primary productivity and phytogeography model, *Global Biogeochem. Cycles*, *9*, 471–490, doi:10.1029/95GB02432.
- Wright, I. J., et al. (2004), The worldwide leaf economics spectrum, *Nature*, *428*, 821–827, doi:10.1038/nature02403.
- Xu-Ri, , and C. Prentice (2008), Terrestrial nitrogen cycle simulation with a dynamic global vegetation model, *Global Change Biol.*, *14*, 1745–1764, doi:10.1111/j.1365-2486.2008.01625.x.
- Zaehle, S., and A. D. Friend (2010), Carbon and nitrogen cycle dynamics in the O-CN land surface model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates, *Global Biogeochem. Cycles*, *24*, GB1005, doi:10.1029/2009GB003521.
- Zaehle, S., S. Sitch, I. C. Prentice, J. Liski, W. Cramer, M. Erhard, T. Hickler, and B. Smith (2006), The importance of age-related decline in forest NPP for modeling regional carbon balances, *Ecol. Appl.*, *16*, 1555–1574, doi:10.1890/1051-0761(2006)016[1555:TIOADI]2.0.CO;2.
- Zaehle, S., P. Friedlingstein, and A. Friend (2010), Terrestrial nitrogen feedbacks may accelerate future climate change, *Geophys. Res. Lett.*, *37*, L01401, doi:10.1029/2009GL041345.
- Zinke, P. J., A. G. Stangenberger, W. M. Post, W. R. Emanuel, and J. S. Olson (1998), *Global Organic Soil Carbon and Nitrogen*, Oak Ridge Natl. Lab. Distrib. Active Arch. Cent., Oak Ridge, Tenn.

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