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# Carbon and nitrogen cycle dynamics in the O-CN land surface model:

## 1. Model description, site-scale evaluation, and sensitivity to parameter estimates

S. Zaehle<sup>1,2</sup> and A. D. Friend<sup>3</sup>

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[1] Nitrogen (N) availability plays a key role in terrestrial biosphere dynamics. To understand and quantify the role of terrestrial N in the Earth system, we developed an advanced terrestrial biogeochemical model O-CN that mechanistically couples terrestrial energy, water, carbon, and nitrogen fluxes in terrestrial ecosystems. We evaluate this new model against observations from intensive forest monitoring plots at temperate and boreal locations in Europe. O-CN simulates realistic foliage N concentrations and N cycling rates and reproduces observed diurnal and seasonal cycles of C fluxes as well as observed gradients in vegetation productivity with N availability for the forest sites studied. A sensitivity test reveals that these results are reasonably robust against uncertainties in model parameter estimates. Using this model we quantify the likely contribution of anthropogenic N deposition to present ecosystem C sequestration as 36 (range: 2–79) g C g<sup>-1</sup> N in agreement with ecosystem manipulation studies.

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### 1. Introduction

[2] Nitrogen (N) availability strongly affects both the productivity of vegetation and the decay of dead organic material. In most pristine temperate and boreal terrestrial ecosystems, N constrains production and biogeochemical fluxes [Vitousek and Howarth, 1991]. This has been demonstrated by the observed enhancement of vegetation growth in N fertilizer addition experiments and field studies on the effects of chronic N deposition [Aber et al., 1998; Matson et al., 2002; Pregitzer et al., 2008]. Field and modeling studies have further suggested an N control on the long-term response of terrestrial ecosystems to climate change and especially to elevated atmospheric CO<sub>2</sub> levels [Luo et al., 2004; de Graaff et al., 2006; Finzi et al., 2007].

[3] A number of recent studies using state-of-the-art terrestrial biogeochemical models in Earth system models have highlighted the importance of terrestrial C sequestration and feedbacks between the terrestrial carbon cycle and the climate system in determining the rate of future climate changes [Cramer et al., 2001; Friedlingstein et al., 2006]. These studies have been criticized for overestimating both future terrestrial C sequestration and the potential carbon-climate feedback because they do not account for N con-

straints [Hungate et al., 2003; Thornton et al., 2007]. However, despite a general appreciation of its importance, the role of N availability in global terrestrial ecosystem and carbon dynamics is still poorly quantified.

[4] This situation results from a number of factors: (1) a lack of mechanistic understanding of terrestrial ecosystem nitrogen and carbon dynamics; (2) insufficient (bio-)geographical data coverage to quantify these dynamics; and (3) the difficulty of quantifying important inputs and outputs, e.g., biological N fixation, and denitrification-based N<sub>2</sub> losses. Previous attempts to account for nitrogen constraints in terrestrial biogeochemical modeling have been limited by the number and detail of N-related processes, and land surface processes in general, that are represented [McGuire et al., 1992; Woodward et al., 1995; Friend et al., 1997; Thornton et al., 2002]. We respond to these challenges in this and an accompanying paper [Zaehle et al., 2010a], where we present and evaluate a newly developed version of the terrestrial biosphere model ORCHIDEE, hereafter O-CN, originally developed by Krinner et al. [2005], with the aim of providing a comprehensive tool to assess the effects of terrestrial N feedbacks on land-atmosphere interactions.

[5] ORCHIDEE represents terrestrial energy, water, and carbon balances for 12 vegetation types and bare soil at an hourly time scale and has previously been used in a range of studies on the interactions between terrestrial biosphere dynamics and climate from seasonal to decadal time scales at local to global levels [Ciais et al., 2005; Piao et al., 2007]. ORCHIDEE is a component of the IPSL Earth system model [Marti et al., 2005], which is designed to study feedbacks between the land surface, atmosphere, and

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oceans [Friedlingstein *et al.*, 2006]. O-CN builds on the ORCHIDEE framework and employs a detailed treatment of foliage N and light to simulate canopy photosynthesis [Friend and Kiang, 2005], a growth model with prognostic calculations of foliage area dynamics considering functional relationships between fine root, foliage mass, and sapwood area (based on the work of Zaehle *et al.* [2006]), and concepts of existing point-scale models of soil organic matter turnover (CENTURY; Parton *et al.* [1993] and Kirschbaum and Paul [2002]) as well as nitrification-denitrification processes (DNDC; Li *et al.* [2000]). A key feature of O-CN is that N concentrations in plant and soil are simulated dynamically, allowing C fluxes (i.e., photosynthesis, autotrophic and heterotrophic respiration, and vegetation turnover) to respond to N status. O-CN treats ecosystem N inputs from atmospheric deposition, biological N fixation, and fertilizer use and mechanistically simulates N losses to leaching and emissions of trace gases resulting from nitrification and denitrification at a half-hourly time step.

[6] Here we evaluate O-CN by comparing key predicted state variables with data from sites with sufficient observations to describe ecosystem nitrogen and carbon fluxes and contents and their responses to atmospheric N inputs and climate. We then quantify the sensitivity of the modeled systems to transient changes in N deposition in comparison to co-occurring changes in climate and atmospheric CO<sub>2</sub>. The model is therefore tested under relatively well-known conditions with respect to both its mean state and response to environmental changes. By analyzing the modeled effects of N deposition on vegetation growth and biogeochemical fluxes, we directly address the current controversy concerning the relative effect of atmospheric N inputs on the long-term forest C balance [Magnani *et al.*, 2007]. Our analyses underpin the regional-scale application and evaluation of O-CN presented in an accompanying manuscript of Zaehle *et al.* [2010a].

[7] Observations from five broadleaved summergreen and seven needleleaved evergreen forest sites along a European transect (41° to 65°N) of climate and N deposition were obtained from the CANIF data set [Schulze, 2000]. These data include annual ecosystem C and N inputs, C and N stocks and turnover. We also obtained observations of hourly gross and net C fluxes from flux towers close to three of these sites from the FLUXNET database [Baldocchi *et al.*, 2001]. FLUXNET data are a standard terrestrial biosphere model benchmark [Friend *et al.*, 2007], and the effects of N feedbacks on the diurnal and seasonal cycles of C fluxes are analyzed for these three sites. It is assumed that similar site conditions between CANIF sites and adjacent FLUXNET sites of the same vegetation type should result in comparable N cycling, and hence a good agreement with observed nutrient use efficiency of production and foliar nitrogen concentrations at the CANIF sites implies an adequate performance at the neighboring FLUXNET site.

[8] Interactions between the carbon and nitrogen cycles introduce feedbacks that could potentially result in strongly nonlinear model behavior, or even instability. The high computational cost of O-CN precludes a full uncertainty

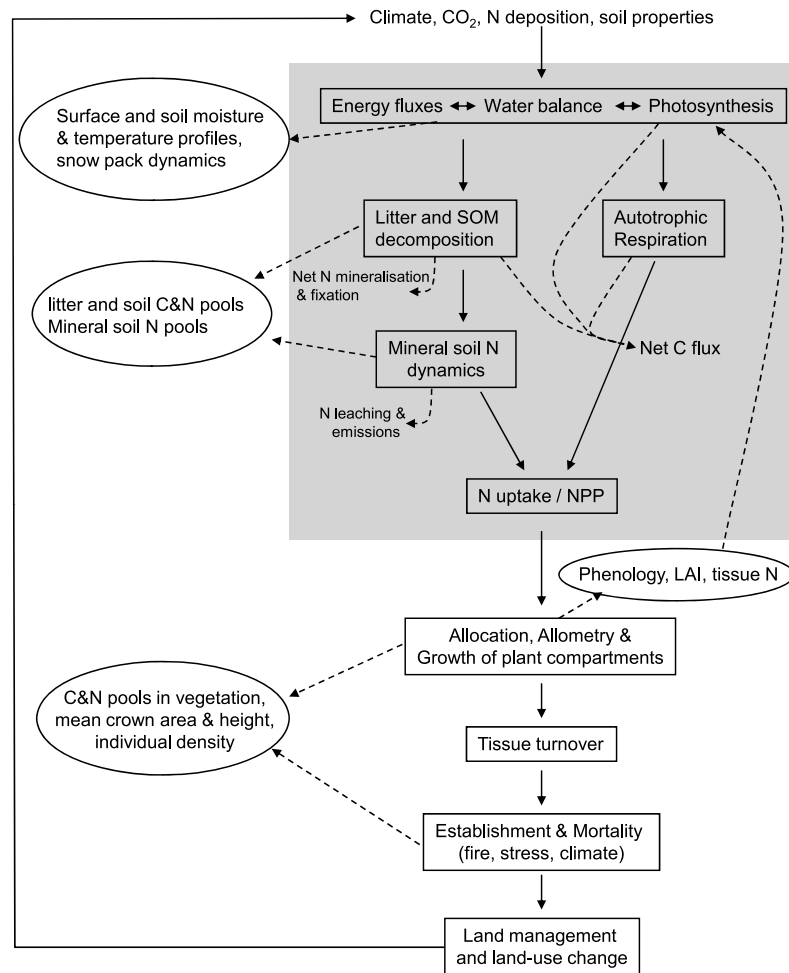
analysis, including interactions between parameter values [Zaehle *et al.*, 2005]. Instead here we vary key model parameters one-at-a-time (OAT) around standard values to investigate the model's sensitivity to its parameterization. Such OAT schemes can identify the main effects of individual parameters and give a first-order estimate of model uncertainty [Saltelli *et al.*, 2000], as well as exposing potential instabilities.

[9] The simulations presented here use no site-specific parameterizations in order to analyze unbiased model behavior relevant to regional to global scales. The same model setup is used for all simulations, and only external parameters (i.e., climate, physical soil properties, N deposition, and vegetation type) are prescribed from observations. We first evaluate mean annual C and N dynamics at 12 boreal and temperate sites taken from the CANIF study, and then evaluate the capacity of the model to reproduce diurnal and seasonal carbon fluxes observed at seven eddy covariance towers (sections 3.1 and 3.2). We test the robustness of the model by systematically varying key parameters related to N processes and vary model input and initialization (section 3.3). Finally, we assess the modeled response of the net ecosystem carbon balance to observed changes in atmospheric CO<sub>2</sub>, N deposition, and climate, with a particular focus on the role of N deposition (section 3.4).

## 2. Methods

### 2.1. Model

[10] O-CN is based on the ORCHIDEE model [Krinmer *et al.*, 2005] but was extended through the addition of key nitrogen cycle processes (Figure 1). ORCHIDEE was conceived as a land surface scheme, linking a soil-vegetation-atmosphere energy and water transfer scheme [de Rosnay and Polcher, 1998] to dynamic models of terrestrial carbon cycling [Viovy, 1996] and vegetation structure [Sitch *et al.*, 2003]. A number of modifications to the original model have been made to facilitate the inclusion of the N cycle. These changes are (1) inclusion of a representation of canopy photosynthesis, based on the work of Friend and Kiang [2005], that explicitly accounts for the N dependence of leaf-level photosynthesis and its integration to canopy-scale carbon and water fluxes; (2) inclusion of a prognostic calculation of the annual maximum foliage area and fine root mass for each vegetation type and each location by replacing the original C allocation scheme, which assumed a vegetation-type specific fixed maximum foliage area [Friedlingstein *et al.*, 1999], with a scheme based on allometric constraints that account for the costs of the growth of a new unit of foliage area due to supporting root and shoot tissues [Shinozaki *et al.*, 1964; Zaehle *et al.*, 2006]; (3) consideration of the dynamics of labile and reserve storage pools to improve modeling of seasonal phenology and to buffer C shortages during times of high respiration demand and low productivity; and (4) calculation of population dynamics through population density and growth-dependent establishment and mortality, as in the work of Sitch *et al.* [2003] and Zaehle *et al.* [2007], while prescribing the maximum fractional coverage of individual plant functional types.



**Figure 1.** Schematic representation of the key processes represented in O-CN. The gray area indicates processes that operate at a time scale of 30 min, whereas the other processes are modeled with a daily time step.

[11] These modifications to the original ORCHIDEE are hereafter referred to as the model version O-C, which does not explicitly account for N constraints on productivity and allocation patterns, but instead assumes that plants were able to maintain tissue N concentrations at observed levels at any time step.

[12] A brief overview of the concepts of the explicit treatment of nitrogen dynamics in O-CN is given here; a full description is given in Text S1.<sup>1</sup> For each plant functional type, and each spatial unit, O-CN balances C and N flows between nine vegetation biomass pools (i.e., foliage, fine roots, aboveground and belowground sapwood and heartwood, fruit organs, and short-term (labile) and long-term storage), six litter pools (i.e., aboveground and belowground metabolic, structural, and woody litter), four soil organic matter pools of differing decomposability, two soil mineral N pools (ammonium and nitrate), and pools of NH<sub>3</sub>, NO<sub>x</sub>, N<sub>2</sub>O, and N<sub>2</sub>. O-CN treats N inputs from reduced and oxidized atmospheric deposition, biological N

fixation, and fertilizer application, and N losses to ammonium and nitrate leaching as well as soil emissions of NH<sub>3</sub>, NO<sub>x</sub>, N<sub>2</sub>O, and N<sub>2</sub>. All transformations and fluxes are calculated on a half-hourly time step with the exception of the daily simulation of vegetation growth and population dynamics.

[13] The growth rate of plants is controlled by their respective labile C and N pool sizes and is subject to allometric constraints. The dynamics of the labile C pool are determined by sinks to tissue growth and autotrophic respiration and C inputs from photosynthesis and a long-term reserve. Autotrophic respiration and photosynthetic rates are dependent on tissue and foliage N concentrations, respectively [Ryan and Waring, 1992; Sitch et al., 2003; Friend and Kiang, 2005], with long-term acclimation mainly controlled by changing investment in tissue N. The dynamics of the labile N pool are determined by the sink of N to tissue growth, internal recycling due to retranslocation at senescence, and long-term storage use, as well as root N uptake. N tissue concentrations are determined prognostically within observed ranges [White et al., 2000] as a function of plant labile N concentration, conserving

<sup>1</sup>Auxiliary materials are available in the HTML. doi:10.1029/2009GB003521.

**Table 1.** Overview of the Model Simulations and Sources of Model Inputs<sup>a</sup>

	Climate	N Deposition	Site Data
Sections 3.1 and 3.3 (“CANIF”)	Observed climatology (1901–2002) [ <i>Mitchell et al.</i> , 2004]	<i>Schulze</i> [2000]	<i>Schulze</i> [2000]
Section 3.2 (“FLUXNET”)	Site meteorology [ <i>Falge et al.</i> , 2005]	TM3 model (1900 to 2000) [ <i>Rhode et al.</i> , 2000; <i>Galloway et al.</i> , 2004]	<i>Falge et al.</i> [2005]
Section 3.4 and Figure 7	Observed climatology (1901–2002) [ <i>Mitchell et al.</i> , 2004]	TM3 model (1900 to 2000) [ <i>Rhode et al.</i> , 2000; <i>Galloway et al.</i> , 2004]	

<sup>a</sup>Historical changes in mean annual atmospheric [CO<sub>2</sub>] were obtained from *Etheridge et al.* [1996] and *Keeling and Whorf* [2006].

relative differences between foliage, fine root, and wood N content [*Friend et al.*, 1997]. Plant N uptake is determined by soil mineral N concentrations, fine root mass, and plant demand for nitrogen [*Kronzucker et al.*, 1995, 1996]. The last is taken to be inversely proportional to plant labile N concentration [*Cardenas-Navarro et al.*, 1999]. Nitrogen availability is known to affect the ratios of foliage and sapwood area to fine root mass [*Brouwer*, 1983; *Poorter and Nagel*, 2000], and as these ratios determine the C cost of a unit foliage area, this implies an N availability constraint on the maximum foliage area during each growing period. In O-CN this C cost occurs through greater below-ground allocation with decreasing labile N concentrations [*Levin et al.*, 1989].

[14] Net N mineralization is taken as the difference between the N released by the decomposition of soil organic matter and the N requirements of litter decomposition, following the CENTURY approach [*Parton et al.*, 1993; *Kirschbaum and Paul*, 2002]. The N content of fresh litter varies with plant tissue N content, reduced by retranslocation, and determines the N requirement to decompose a unit of litter and the rate at which the litter decomposes through an assumed relationship between tissue N and lignin content. C:N ratios of soil organic matter decline as soil mineral N concentrations increase using empirical functions [*Parton et al.*, 1993]. Site-level biological N fixation is estimated from long-term mean climate using a relationship based on the work of *Cleveland et al.* [1999]. Formulations to estimate nitrification of ammonium to nitrate, denitrification of nitrate, and associated gaseous losses to NH<sub>3</sub>, NO<sub>x</sub>, N<sub>2</sub>O, and N<sub>2</sub> have been adapted from *Li et al.* [2000]. Ammonium and nitrate leaching is calculated in proportion to their respective concentrations and simulated water loss from the soil profile. Soil concentrations of ammonium and nitrate are thus determined from the balance of N inputs due to deposition of NH<sub>x</sub> and NO<sub>y</sub>, biological N fixation, net N mineralization, and N losses to leaching and gaseous emissions associated with nitrification and denitrification processes, as well as plant ammonium and nitrate uptake.

## 2.2. Data

[15] Data characterizing aboveground C and N productivity, tissue N concentrations, and N stocks in 12 broad-leaved summergreen and needleleaved evergreen forest ecosystems along a gradient in climate and nitrogen deposition were obtained from the CANIF data set [*Schulze*, 2000]. The data available also comprise essential site

characteristics such as soil texture, soil pH, dry and wet reduced and oxidized N deposition estimates, and vegetation type. Because only mean climate information is available, time series of temperature, precipitation, surface humidity, cloudiness, and surface wind speed were obtained for the nearest 0.5° grid cell in the CRU climatology [*Mitchell et al.*, 2004], and used to force O-CN.

[16] Three of the intensive monitoring plots were identical to, or very close to, eddy covariance measurement sites in the FLUXNET database [*Baldocchi et al.*, 2001; *Falge et al.*, 2005]. Measured half-hourly net CO<sub>2</sub> fluxes, and meteorological conditions were obtained from these three sites to analyze modeled diurnal and seasonal simulated carbon fluxes. Gross primary productivity (GPP) was estimated by separating the net CO<sub>2</sub> flux into canopy C uptake and total ecosystem respiration (TER), including canopy respiration, using the method of *Reichstein et al.* [2005]. TER was derived by fitting an Arrhenius-type temperature response function to binned night-time air temperatures and u\*-filtered net CO<sub>2</sub> fluxes with a 15 day moving window. For days in which the curve fitting procedure did not produce reliable or realistic parameter estimates (typically ~10% of the days, but up to 50% at individual sites), mean parameters for valid days were used. Days with >70% of reliable data were used to construct a time series of daily net ecosystem production (NEP) and GPP, from which mean summer diurnal and seasonal cycles were calculated.

## 2.3. Modeling Protocol

[17] All simulations are performed following the same modeling protocol using the model forcing described in Table 1. Litter and soil organic matter are initialized based on the ratio of mean annual potential evaporation to precipitation [*Friend and White*, 2000, equation 3]. The model is then run to equilibrium with respect to C and N fluxes and stocks using preindustrial climate, N deposition, and CO<sub>2</sub> as driving variables. To increase the speed of convergence to equilibrium, a 30 year mean seasonal cycle of litter fall and its C:N stoichiometry, as well as soil temperature and moisture, is calculated every 100th simulation year. This mean seasonal cycle is used to simulate soil organic matter dynamics separately from vegetation for 1000 model years to bring the slow turnover pools into equilibrium with their inputs. Following this procedure, and starting from equilibrium conditions of both vegetation and soil pools, a transient simulation is performed using historical climate, N deposition, and atmospheric CO<sub>2</sub> from 1860

**Table 2.** Coordinates, Vegetation Type, Nitrogen Deposition Rates, and Key Model Predictions for the 12 CANIF Sites<sup>a</sup>

SITE	Lat	Lon	PFT	NDEP (kg N ha <sup>-1</sup> a <sup>-1</sup> )	NPP (g C m <sup>-2</sup> a <sup>-1</sup> )	N <sub>foliage</sub> (%)	N <sub>up</sub> (g N m <sup>-2</sup> a <sup>-1</sup> )	N <sub>min</sub> (g N m <sup>-2</sup> a <sup>-1</sup> )
Ahe <sup>b</sup>	64°13′	19°30′	BNE	1.9	646 ± 25	0.84 ± 0.02	5.5 ± 1.7	5.5 ± 0.9
AuF	48°12′	7°11′	TeBS	15.0	846 ± 39	2.13 ± 0.05	15.2 ± 2.3	14.0 ± 2.1
AuP	48°12′	7°11′	TeNE	15.0	1006 ± 28	1.11 ± 0.03	10.3 ± 2.7	9.5 ± 2.3
Col	41°52′	13°38′	TeBS	10.8	652 ± 101	2.34 ± 0.06	13.6 ± 1.9	12.3 ± 1.4
Gri <sup>c</sup>	55°58′	12°15′	TeBS	12.6	774 ± 68	2.08 ± 0.11	13.6 ± 2.9	12.6 ± 2.9
Jez	50°33′	13°28′	TeBS	20.8	737 ± 106	2.22 ± 0.05	14.1 ± 2.4	12.4 ± 2.1
Klo	56°29′	8°24′	TeNE	20.6	961 ± 22	1.14 ± 0.02	10.1 ± 1.6	8.9 ± 1.4
MdM	41°45′	14°53′	TeNE	10.4	800 ± 106	1.30 ± 0.03	9.1 ± 2.3	8.1 ± 2.1
Nac	50°35′	13°15′	TeNE	17.8	938 ± 78	1.15 ± 0.09	9.7 ± 2.3	8.3 ± 2.8
Sch	50°04′	11°50′	TeBS	19.5	767 ± 79	2.11 ± 0.08	13.6 ± 2.5	11.8 ± 2.4
Sko	56°33′	13°13′	TeNE	15.4	909 ± 33	1.00 ± 0.04	9.0 ± 1.8	8.1 ± 1.6
Wal <sup>d</sup>	50°12′	11°53′	TeNE	20.1	976 ± 223	1.08 ± 0.08	9.6 ± 2.3	8.2 ± 2.4

<sup>a</sup>Coordinates are °N and °E, and nitrogen deposition (NDEP) rates are from 1996–1999 [Schulze, 2000]. The 1990s annual mean ± standard deviation of net primary production (NPP), foliage N (N<sub>foliage</sub>), plant N uptake (N<sub>up</sub>), and net N mineralization (N<sub>min</sub>). Sites and their codes: Åheden (Ahe), Aubere (AuF, AuP), Collelongo (Col), Gribskov (Gri), Jezeri (Jez), Klosterhede (Klo), Monte di Mezzo (MdM), Nacetin (Nac), Schacht (Sch), Skogaby (Sko), and Waldstein (Wal). Plant functional types are prescribed for each site and defined as: BNE: Boreal needleleaved evergreen forest; TeBS: Temperate broadleaved summergreen forest; TeNE: Temperate needleleaved evergreen forest.

<sup>b</sup>Close to the eddy-covariance site of Flakaliden.

<sup>c</sup>Close to the eddy-covariance site of Sorø.

<sup>d</sup>Close to the eddy-covariance site of Weidenbrunnen.

to 2000. No account is taken of the effects of land use or disturbances such as wind-throw or fire.

[18] A one-at-a-time (OAT) sensitivity analysis is performed following the same protocol for three representative sites (i.e., Åheden, Gribskov, and Waldstein) by modifying key N-related model parameters (see Tables S1 and S2 for definition of the parameters) controlling the following model attributes: root N uptake ( $v_{\max}$ ,  $K_{N\min}$ ); vegetation growth N use efficiency ( $nf$ ,  $r_m$ ); N effect on vegetation structure ( $k_{N\text{alloc}}$ ); dynamics of tissue N concentrations ( $D_{\max}$ ,  $f_{\text{trans}}$ ,  $nc_{\text{leaf,min}}$ ,  $nc_{\text{leaf,max}}$ ); the fractions of N losses to leaching and emissions ( $f_{\text{leach}}$ , soil pH, which strongly affects NH<sub>4</sub> sorption and denitrification rates); soil organic matter N concentrations ( $NC_{\text{soil}}$ ; determining the amount of N required or released to decompose a unit of soil C and thus affecting competition between soil microbes and vegetation); N input (biological nitrogen fixation (BNF)); and the initialization of soil organic matter ( $C_{\text{init}}$ ). Parameters are modified individually by ±10% (except for pH, which was modified by ±0.1), keeping all other parameters at default values.

[19] Finally, to provide an assessment of the effect of N deposition on net ecosystem production covering a wide range of boreal and temperate climates and N deposition rates, the set of 12 CANIF sites was extended by a set of 75 additional European and North American temperate and boreal forest sites, for which observation-based estimates of gross and net primary production are available through the database of Luyssaert *et al.* [2007]. The marginal effect of N deposition was inferred as the difference between a simulation accounting for the historic changes in N deposition, atmospheric CO<sub>2</sub> and climate, and a simulation in which only atmospheric CO<sub>2</sub> and climate are changed.

### 3. Results

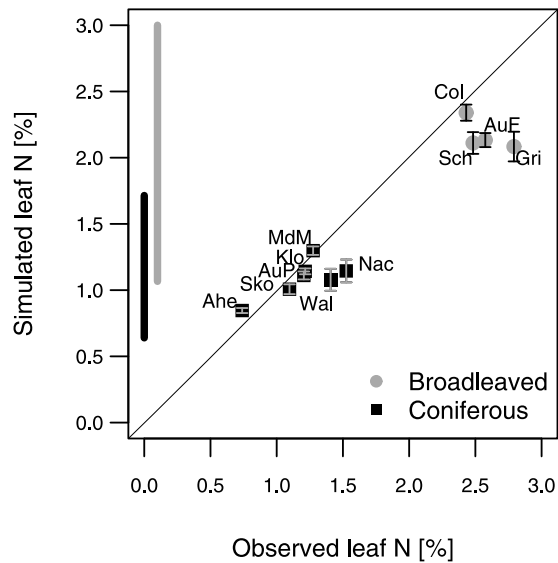
#### 3.1. Nitrogen Status

[20] Table 2 summarizes key simulated characteristics of the CANIF forest sites. To assess the ability of O-CN to

correctly simulate N fluxes, concentrations, and effects across different vegetation types, climates, and N inputs, three indicators are used: (1) foliage N concentration, closely linked to all plant tissue N concentrations and to the nitrogen stress experienced by the vegetation, and which affects both the photosynthetic capacity and respiration rates; (2) nitrogen use efficiency of vegetation growth, which integrates plant N concentrations and the response of both photosynthetic capacity per unit leaf area and relative allocation to leaves, fine roots, and woody biomass to N availability; and (3) the ratio of internal ecosystem N recycling to N inputs, i.e., the number of times N is cycled between vegetation and soil, to give an indication about the change in openness of the N cycle with N deposition and climate.

[21] Figure 2 shows that O-CN predicts foliage N concentrations that are in general agreement with measurements at the 12 CANIF sites. The modeled concentrations are subject to a comparatively small interannual variation, shown as bars in Figure 2. Modeled foliage N concentrations furthermore exhibit a weak seasonal cycle (not shown), with a decrease over the course of the growing season of about the same magnitude as the interannual variations. This decrease in foliage N concentrations over the growing season is generally consistent with the observations of Kull *et al.* [1998] on two *Salix* species.

[22] Simulated foliage N falls in the middle of the range of the empirically determined and imposed constraint minimum and maximum concentrations for both needleleaved and broadleaved leaf types, indicated by the bars on the left in Figure 2. The choice of the parameter values determining upper and lower bounds of foliage N concentrations affect this result, but are not its major cause (see section 3.3). Rather, the in-built relationships between N availability, N uptake, nitrogen use efficiency, and allocation patterns play a decisive role in modeling foliage N concentrations. O-CN captures the general trend toward higher foliage nitrogen concentrations with increasing atmospheric N deposition in conifers (Table 2 and Figure 2). However, most of the



**Figure 2.** Simulated versus observed foliage nitrogen concentrations at the 12 CANIF sites. The black and gray bars on the left denote the permissible range of simulated foliage nitrogen concentrations for needleleaved evergreen and broadleaved summergreen PFTs, respectively. The error bars denote the standard deviations of the average annual foliage N concentrations (1991–2000).

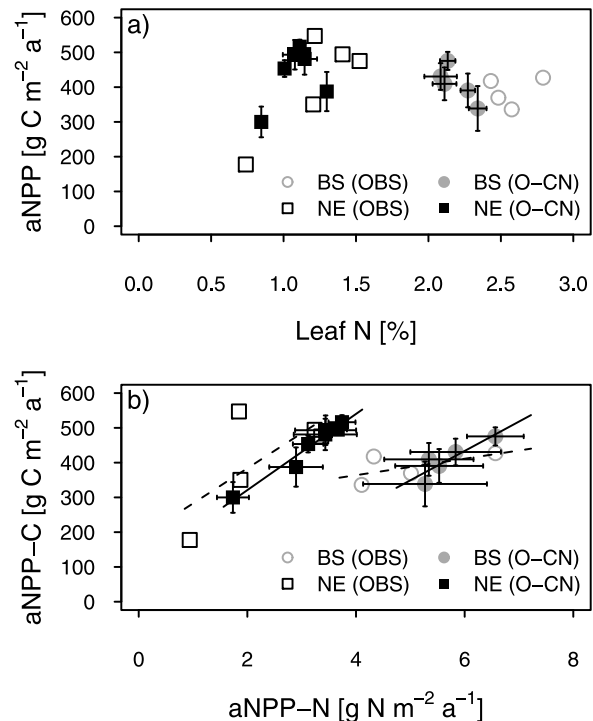
observed between-site variation within a plant functional type is not captured by the model. In particular, the simulated foliage N concentrations for the broadleaved PFT are systematically lower than those reported for beech trees by *Schulze* [2000]. This could indicate a too weak N constraint on C growth in broadleaved trees, although it should be recognized that the reported foliage N concentrations are at the high ends of the ranges reported by two other, independent data sets for a wider range of broadleaved tree species [*White et al.*, 2000; *Wright et al.*, 2004].

[23] Despite its role in determining photosynthetic capacity on a leaf area basis, foliage N concentrations are only very weakly correlated net primary production in both observations and model results (Figure 3a). Conifers attain a level of aboveground productivity comparable to broadleaved forest but with lower levels of foliage N concentrations. This can be partly explained by the wider C:N ratios of the living biomass in needleleaved evergreen trees, and the compensating effects of lower specific leaf area and higher leaf longevity in conifers, leading to similar or higher total canopy N content per unit of foliage and ground area. Aboveground nitrogen use efficiency, defined as ratio of aboveground net C productivity and net C productivity, ranges 64–76 (observed: 65–95)  $\text{g C g}^{-1} \text{N}$  in broadleaved summergreen, and 133–172 (observed: 141–189)  $\text{g C g}^{-1} \text{N}$  in needleleaved evergreen forests (Figure 3b). This good agreement with observations suggests that the model captures well the magnitude and major differences in N dynamics between needleleaved and broadleaved trees, and their many interactions with C uptake and partitioning.

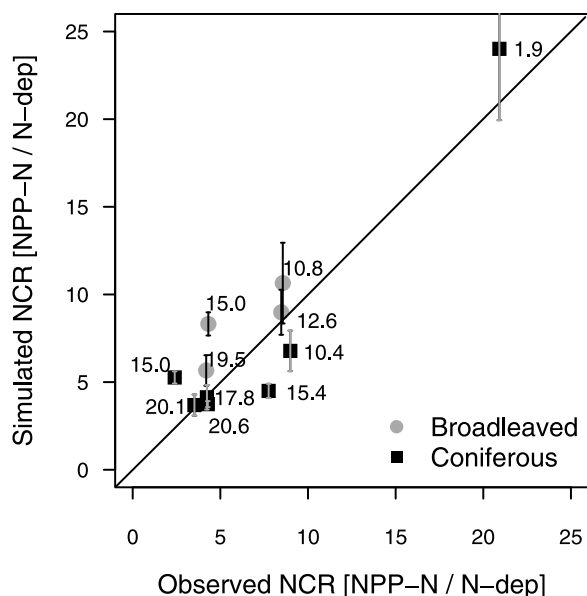
[24] Simulated vegetation N uptake is tightly controlled by net N mineralization (Figure S1). Observations of net

nitrogen mineralization are not available for all sites, but the model-based estimates for temperate needleleaved evergreen ( $8.1 \text{ g N m}^{-2} \text{ a}^{-1}$ ) and temperate broadleaved summergreen forests ( $12.6 \text{ g N m}^{-2} \text{ a}^{-1}$ ) are close to the average over the sites where such data are available (i.e.,  $9 \text{ g N m}^{-2} \text{ a}^{-1}$  and  $13 \text{ g N m}^{-2} \text{ a}^{-1}$  for temperate coniferous and broadleaved sites, respectively). No net nitrogen mineralization was detectable at the boreal site, whereas the model estimates about  $5 \text{ g N m}^{-2} \text{ a}^{-1}$ , a rate necessary to sustain the simulated rate of growth.

[25] The nitrogen cycling ratio (NCR) is defined as the ratio between N uptake by the vegetation (taken as aboveground NPP-N due to the lack of data availability for fine root mass) and ecosystem N input (observed atmospheric deposition of  $\text{NH}_x$  and  $\text{NO}_y$ , discounting for the contribution of biological N fixation due to the lack of observations), i.e.,  $\text{g N}_{\text{uptake}} \text{ g}^{-1} \text{N}_{\text{input}}$ . NCR therefore represents the mean number of times an atom of N from N deposition is taken up by the vegetation before being lost to either leaching or emissions. Figure 4 shows that O-CN captures the overall difference in magnitude between the NCR for the boreal needleleaved forest site (20.9 and 24.0 observed and modeled, respectively), temperate needleleaved forest sites ( $5.2 \pm 2.6$  and  $4.7 \pm 1.2$  observed and modeled, respectively), and temperate broadleaved forest sites ( $6.4 \pm 2.5$  and  $7.8 \pm 2.2$  observed and modeling, respectively), as



**Figure 3.** Observed and simulated aboveground net carbon primary productivity (NPP-C:  $\text{g C m}^{-2} \text{ a}^{-1}$ ) as a function of (a) foliage nitrogen concentration (percent of dry matter) and (b) aboveground net nitrogen primary productivity (NPP-N:  $\text{g N m}^{-2} \text{ a}^{-1}$ ). Regression lines are based on linear regressions. BS, broadleaved summergreen PFT; NE, needleleaved evergreen PFT.



**Figure 4.** Simulated versus observed nitrogen cycling ratio, defined as the ratio of annual net nitrogen primary productivity to annual nitrogen deposition, for the 12 CANIF sites. Numbers denote the observed average N deposition ( $\text{kg N ha}^{-1} \text{a}^{-1}$ ) at each site, 1996–1999.

well as the trend for increasing NCR with decreasing N deposition within both needleleaved and broadleaved groups. Despite these encouraging features, O-CN does not reproduce most differences between sites with similar climate and nitrogen inputs, which may be related to soil fertility or site history.

[26] The lower NCR in temperate ecosystems is indicative of a larger difference between on the one hand the total mineral N production rate of the simulated ecosystems resulting from net N mineralization, N deposition, and biological N fixation, and on the other hand the rate of vegetation N uptake, in temperate forest sites. This difference results from an increasing fraction of N circulating in these ecosystems is lost due to leaching and gaseous emissions. Unfortunately no adequate measurements of N losses are available for these sites to evaluate this trend. Notably, N deposition is not correlated with the higher simulated and observed rates of N mineralization in broadleaved ecosystems.

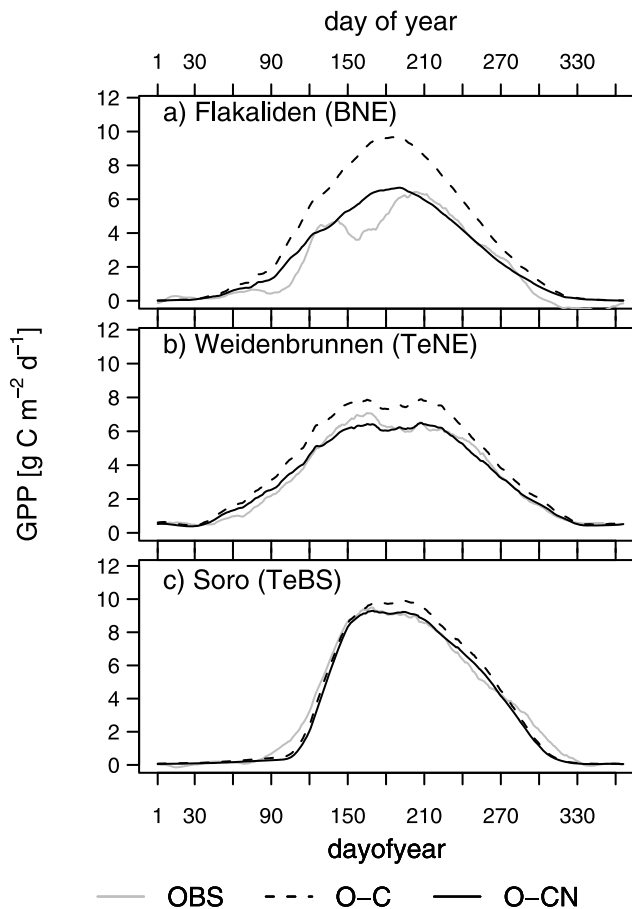
### 3.2. Diurnal and Seasonal Cycles of Carbon Fluxes

[27] The capacity of O-CN to reproduce observed diurnal and seasonal cycles of net ecosystem production (NEP) and gross primary production (GPP) is tested for three eddy covariance measurement sites. To disentangle the effects of the representation N-related processes from any other model deficiencies, an additional model simulation was performed using the O-C model that does not explicitly account for nitrogen availability.

[28] Generally, O-CN performs well with respect to correlation coefficients and root-mean-squared errors for all the sites. Figure 5 (Figure S2) demonstrates this for the average seasonal cycle of GPP (and NEP, respectively) for

the eddy-covariance sites close to the sites used for section 3.1: Flakaliden, close to the boreal needleleaved evergreen site of Åheden; Weidenbrunnen, close to the temperate needleleaved evergreen site of Waldstein; and Sorø, close to the temperate broadleaved summergreen site of Gribskov. The observed mean summertime diurnal cycles of net and gross C fluxes are confidently reproduced by O-CN (results not shown).

[29] Explicitly accounting for the effects of N availability on plant structure, growth, and soil organic matter decomposition does not change the shape of either the simulated diurnal or seasonal cycle of carbon fluxes. The simulated cycles of GPP and NEP at the Weidenbrunnen and Sorø temperate forest sites indicate no simulated strong N limitation, and therefore O-C and O-CN produce similar predictions. At the boreal site (Flakaliden), however, low nitrogen availability reduces leaf area index and foliar N concentrations. These two factors are the main cause for the reduction of the seasonal amplitude of the carbon fluxes in



**Figure 5.** Average observed and simulated seasonal cycle of gross primary productivity (GPP) at (a) Flakaliden ( $r^2$ : 0.68(0.67), RMSE: 2.3(3.9)  $\text{g C m}^{-2} \text{d}^{-1}$ ), (b) Weidenbrunnen ( $r^2$ : 0.85(0.85), RMSE: 1.1(1.8)  $\text{g C m}^{-2} \text{d}^{-1}$ ), and (c) Sorø ( $r^2$ : 0.94(0.94), RMSE: 1.0(1.2)  $\text{g C m}^{-2} \text{d}^{-1}$ ). Statistics are given for O-CN (O-C) and have been calculated using daily values; plotted values are a 30 day running mean. RMSE is the root-mean-squared error.



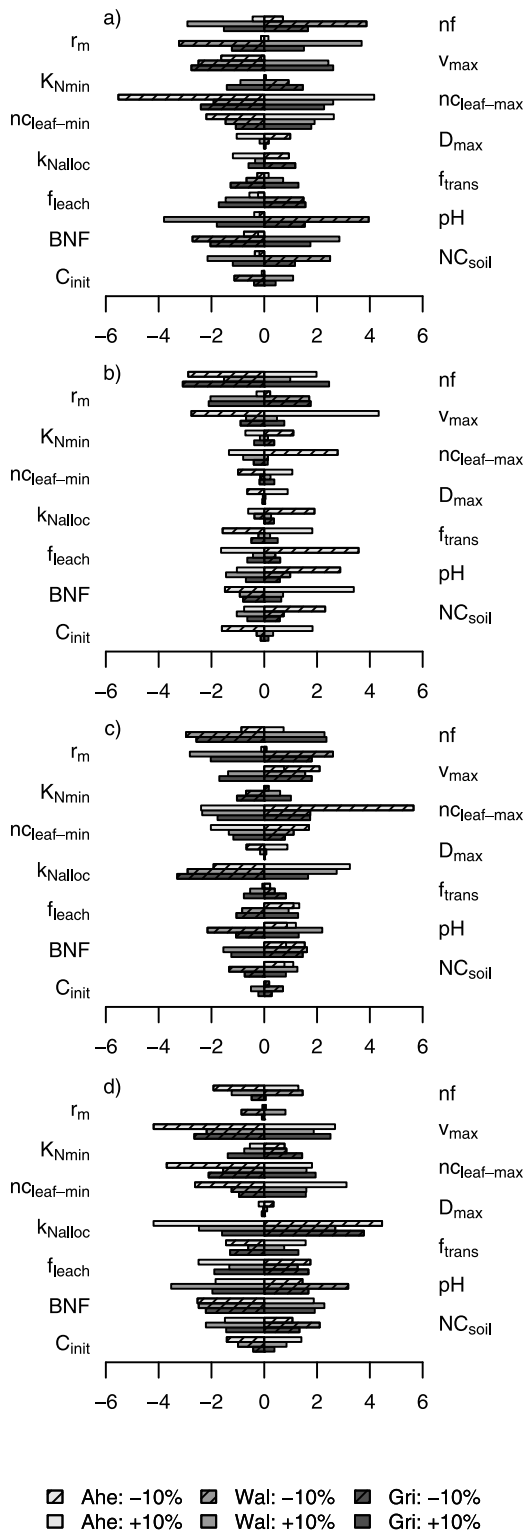
comparison to O-C, substantially improving the fit to the observations. These results suggest that O-CN produces reasonable predictions across a gradient of N availability. Inclusion of dynamic N thus allows simulating the lower boreal productivity without requiring modifications of foliage N concentrations and allocation factors specific for boreal conditions.

### 3.3. Sensitivity of Model Results to Parameter Estimates

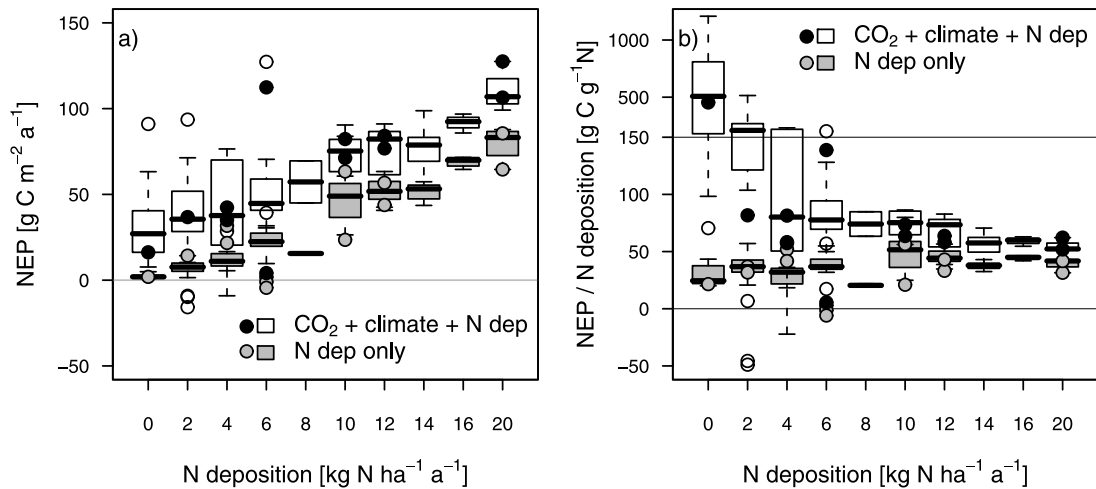
[30] Figure 6 shows the sensitivity of simulated foliage N, net primary productivity, nitrogen use efficiency and nitrogen cycling ratios to uncertainty and potential errors in model parameterization. Simulated foliage N concentrations vary by about 3% relative to the simulated concentration in the default model parameterization, with a maximum change of 5.7%, or 0.07% in absolute terms (Figure 6a). Foliage N is slightly more sensitive to the upper bound ( $nc_{\text{leaf,max}}$ ) than the lower bound ( $nc_{\text{leaf,min}}$ ), reflecting the difference in the absolute magnitude of change corresponding to a relative change by 10%. The elasticity parameter  $D_{\text{max}}$  that assures a smooth development of foliage N content has hardly any effect on mean foliage N concentration. Parameters affecting the root nitrogen uptake strength ( $v_{\text{max}}$ ,  $K_{\text{Nmin}}$ ), defining the relative competitiveness of plants versus soil microbes for mineral soil N, and parameters affecting the N use efficiency of photosynthesis ( $nf$ ) and respiration ( $r_m$ ) also play an important role in determining foliage N.

[31] Net primary productivity (NPP, Figure 6b) is predominantly controlled by the leaf-level nitrogen use efficiency parameter ( $nf$ ), determining the rate of photosynthesis per unit leaf N, and the respiration rate per unit tissue nitrogen parameter ( $r_m$ ), with parameters affecting the N inputs or outputs being more important at the nutrient stressed boreal site (Ahe). Nitrogen use efficiency (NUE, Figure 6c), i.e., NPP-C divided by NPP-N, responds typically by less than 3% to parameter changes. Notably, the choice of the upper and lower bounds of foliage N ( $nc_{\text{leaf,max}}$ ,  $nc_{\text{leaf,min}}$ ) do not substantially alter the predictions, with exception of a decrease in  $nc_{\text{leaf,max}}$  at the boreal site causing a 5.7% relative increase in NUE, or  $10 \text{ g C g}^{-1} \text{ N}$  in absolute terms.

[32] The lifetime of N in the system, i.e., the N cycling ratio, is influenced to an about equal extent by parameters affecting vegetation growth and those affecting gaseous or leaching losses (pH,  $f_{\text{leach}}$ ), and typically varies by less than 4% around the value obtained with the standard parameter-



**Figure 6.** Relative change in simulated 1990s (a) average foliage N concentration, (b) net primary production, (c) nitrogen use efficiency, and (d) nitrogen cycling ratio from varying one model parameter at a time (see section 2.3). Simulation results are shown for the three intensive study sites of Åheden (Ahe), Waldstein (Wal), and Gribskov (Gri). Parameters:  $nf$ , nitrogen use efficiency of photosynthesis;  $r_m$ , maintenance respiration coefficient;  $v_{\text{max}}$ , maximum root N uptake capacity;  $K_{\text{Nmin}}$ , half-saturation concentration of plant N uptake;  $nc_{\text{leaf-min/max}}$ , minimum and maximum permitted foliage N concentration, respectively;  $D_{\text{max}}$ , maximum elasticity of foliar N concentration;  $k_{\text{Nalloc}}$ , slope of the allocation response to N limitation;  $f_{\text{trans}}$ , fraction of N retranslocated before shedding;  $f_{\text{leach}}$ , proportionality constant of leaching loss to soil water content; pH, soil pH; BNF, biological nitrogen fixation;  $\text{NC}_{\text{soil}}$ , N concentration of soil organic matter at  $1 \text{ g soil mineral N m}^{-2}$ ; and  $C_{\text{init}}$ , initial soil C stock ( $\text{g C m}^{-2}$ ). See Text S1 and Tables S1 and S2 for parameter descriptions.



**Figure 7.** The 1990s average (a) net ecosystem productivity (NEP) and (b) ratio of NEP over the change of N deposition from preindustrial values (1990s versus 1900s) for the 12 CANIF sites (filled circles) and 87 temperate and boreal forest sites, including the 12 CANIF sites (boxes, whiskers, and open circles). Values are reported for a simulation accounting for historical changes in N deposition, climate, and atmospheric  $\text{CO}_2$ , as well as resulting from the historical changes in N deposition only.

ization. Parameter uncertainty in net ecosystem production (NEP) is not associated with any specific parameter across the three sites (*results not shown*), and does affect neither the sign nor the order of magnitude of estimated net C uptake. The effect of the uncertainty (average:  $5 \text{ g C m}^{-2} \text{ d}^{-1}$ ) is substantially lower than the effect of interannual climate variability (average:  $83 \text{ g C m}^{-2} \text{ d}^{-1}$ ) on NEP.

[33] Most parameter sensitivities resulting from the 10% perturbation are lower than the interannual variability of the variable in question. The model response is for most parameters and variables of a comparable magnitude in both directions of the change, and we did not observe any instability of the model results as a consequence of model parameterization changes. Altogether this leads to the conclusion that the results are reasonably robust to uncertainty and potential errors in model parameterization. Uncertainty in the initial soil carbon pool,  $C_{\text{init}}$ , has only very moderate effect on the final model result.

### 3.4. Effects of N Deposition on Forest C and N Fluxes and Its Contribution to Present-Day C Sequestration

[34] We now exploit the capacity of O-CN to simulate realistic rates of C and N cycling for the sites analyzed, and the relative robustness of simulated NEP values for analysis of the effect of historical changes in atmospheric N deposition on forest C cycling. To obtain a larger sample of climate and nitrogen deposition levels in temperate and boreal ecosystems, we extend the analysis to 75 additional forest sites, giving a total of 87 sites (section 2.2). *Zaehle et al.* [2010a] have demonstrated a satisfactory data-model agreement in terms of gross and net primary production with mean vegetation type estimates of this data set. For the sites used here, O-CN simulates a mean Euclidean error (MEE; *Li and Zhou* [2006]) in GPP of  $376 \text{ g C m}^{-2} \text{ a}^{-1}$  (rMEE: 0.75) and  $202 \text{ g C m}^{-2} \text{ a}^{-1}$  in NPP (rMEE: 0.69),

where rMEE is the ratio of the MEE with the standard deviation of the observations.

[35] Figure 7a shows that there is a rather linear increase in simulated NEP with increasing N deposition. This is true irrespective of whether only the historical changes in N deposition or the effects of covarying climate and  $\text{CO}_2$  are taken into account. The response of the net C uptake to N deposition is about  $36$  (range: 2 to  $79$ )  $\text{g C g}^{-1} \text{ N}$  deposited; and remarkably stable across the entire range of N deposition considered here (Figure 7b). Most N added from N deposition is sequestered in soil organic matter, with minor increases in mineral soil N concentrations, and with only little additional N stored in vegetation. At only few sites, increased mineral soil N concentrations leads to noticeable additional N losses, and for all sites these losses remain substantially smaller than the additional N inputs and sequestration.

[36] Evergreen needleleaved forests have a tendency to respond more to N deposition (in terms of both NPP and NEP) than broadleaved summergreen forest sites with a similar climate and N deposition rate. For example, the 1990s mean NEP related to N deposition at AuP and AuF is  $85 \text{ g C m}^{-2} \text{ a}^{-1}$  (needleleaved evergreen) and  $65 \text{ g C m}^{-2} \text{ a}^{-1}$  (broadleaved summergreen). This vegetation type effect on the N deposition related NEP is still visible, but less marked (needleleaved:  $60 \pm 17 \text{ g C m}^{-2} \text{ a}^{-1}$ , broadleaved:  $49 \pm 22 \text{ g C m}^{-2} \text{ a}^{-1}$ , mean over sites and its standard deviation) when taking account of all sites with significantly elevated N deposition, taken here as  $>10 \text{ kg N ha}^{-1} \text{ a}^{-1}$ . The main explanation for the difference in the response of sites is related to their initial N availability and its relative increase due to N deposition. The difference results from the higher nitrogen use efficiency and the lower simulated C:N ratio of needleleaved tissues, as well as the relative advantage of additional N for evergreen trees due to reduced below-

ground investment because of their higher foliage longevity in comparison to summergreen trees.

[37] Concurrent changes in atmospheric CO<sub>2</sub> concentration and climate tend to increase simulated NEP, mainly as a consequence of the CO<sub>2</sub> fertilization effect. This is reflected in a much higher apparent response of the net C uptake to N deposition, when the simulated 1990s net C uptake is expressed as relative to the 1990s N deposition (Figure 7b).

## 4. Discussion

### 4.1. Model Evaluation at the Site Scale

[38] Evaluation of a complex ecosystem model designed for global applications is challenging. Few data sets report complete vegetation and soil C and N stocks and fluxes, far fewer than the growing number of intensive C-cycling monitoring plots. Moreover, establishing the useful information content of site-level observations for evaluating a global model is not straightforward. Observed patterns are influenced by site-specific conditions such as site history and soil fertility, as discussed by *Thornton et al.* [2002] and *Zaehle et al.* [2006], that are difficult to capture adequately in global-scale models. In addition, the measurements themselves are subject to considerable, usually unknown, uncertainty, resulting from difficulties in establishing quantities such as fine root mass and turnover, or net nitrogen mineralization [*Schulze*, 2000; *Clark et al.*, 2001]. We therefore concentrated our model evaluation to replication of mean behavior over sites with similar climate and N input characteristics rather than attempting to assess between-site variation. Figure 7 shows that the 12 CANIF sites encompass well the entire range of N deposition and simulated NEP responses of the wider selection of sites, which in hindsight lends some support for the choice of these 12 sites for evaluating the carbon and nitrogen cycles of O-CN in boreal and temperate forest ecosystems.

[39] The results presented here demonstrate that the inclusion of key N dynamics parameterizations within the ORCHIDEE land surface scheme has been successful. That is, the level of correspondence between modeled and observed quantities inspires confidence in the ability of the model to help understand and predict real world C-N interactions. The model simulates realistic ranges of N tissue concentrations, N use efficiencies, net N mineralization, and N turnover rates for the temperate and boreal sites studied, and for which key components have been measured. We have concentrated on sites with more or less complete N stock estimates and quantified N cycling rates, which has limited the number of boreal sites. More data on individual N cycle components exist from other sites and scales, and these are used in an accompanying paper to further evaluate the model performance, which also extends the evaluation to tropical ecosystems [*Zaehle et al.*, 2010a].

[40] Including terrestrial N processes in O-CN results in equivalent or improved model performance in comparison with the eddy-covariance data used for benchmarking the original ORCHIDEE model as described by *Krinner et al.* [2005]. The model does not account for site history, which significantly affects the observed net ecosystem exchange at young forest sites [e.g., *Kolari et al.*, 2004; *Kowalski et al.*,

2004]. It is thus not surprising that the simulated NEP, accounting for only changes in atmospheric CO<sub>2</sub> levels, atmospheric N input, and climate is closer to zero than observed at these managed sites. Separating the net C flux into the constituent fluxes GPP and TER enables a more precise model evaluation, and can thus be used to examine daily and seasonal cycles of site-level ecosystem productivity. GPP estimates derived through flux separation from observed NEP using different methods for calculating TER generally agree within 10% [*Desai et al.*, 2008], suggesting that these data provide a reliable source of information for model evaluation.

[41] Accounting for N dynamics requires a large increase in the number of represented processes and introduces feedback mechanisms and nonlinear model behavior, which potentially could cause model instability. The results in section 3.3 demonstrate that this is not the case. Rather, changes in parameters result in small and in most cases linear changes in model outcomes. The uncertainty resulting from these parameter perturbations is in most cases smaller than the interannual variability of the model result, which implies that key predictions of the model, such as the N constraint on net primary production and net ecosystem production can be confidently interpreted. Key sensitive vegetation parameters are the nitrogen use efficiency parameter of photosynthesis ( $\eta_f$ ), and the maximum root N uptake rate per unit root mass ( $v_{\max}$ ), each defining important physiological carbon-nitrogen linkages. It is probable that  $\eta_f$  can be constrained in different plant types by a combination of eddy-covariance data, leaf N measurements, and additional plant trait data [e.g., *Kattge et al.*, 2009]. Given the difficulties of belowground measurements, the quantification of root nitrogen uptake capacity under field conditions at the plot scale or larger will remain challenging.

[42] A key challenge in modeling terrestrial ecosystem N fluxes remains the quantifying of N inputs and outputs. Average daily emission rates of NO and N<sub>2</sub>O at the 12 CANIF sites calculated by O-CN, 0.34 and 0.09 g N m<sup>-2</sup> a<sup>-1</sup>, respectively, are similar to values observed across European forest sites: 0.43 (range: 0 to 1.17) and 0.15 (range: 0.004 to 0.66) g N m<sup>-2</sup> a<sup>-1</sup>, for NO and N<sub>2</sub>O, respectively [*Kesik et al.*, 2005]. Simulated N leaching rates average, over temperate sites, 0.48 g N m<sup>-2</sup> a<sup>-1</sup>, which compares favorably with reported average rates in German temperate forest sites of 0.43 g N m<sup>-2</sup> a<sup>-1</sup>, reaching a maximum of 1.01 (modeled) and 2.7 g N m<sup>-2</sup> a<sup>-1</sup> (observed) [*Brumme and Khanna*, 2008]. However, such comparisons are only of an indicative nature because of the high spatial and temporal variability in these losses, rather than a thorough evaluation of the predicted fluxes. We are continuing to evaluate O-CN using in situ observations of N trace gas emissions in a related study.

### 4.2. Effect of N Deposition and Increasing Atmospheric CO<sub>2</sub> on Simulated N Cycling and Net Ecosystem Productivity

[43] A major stimulus for the development of O-CN has been the desire to understand and predict potential N constraints on the responses of terrestrial ecosystems to present and future environmental change [e.g., *Hungate et*

*al.*, 2003; *Magnani et al.*, 2007; *Thornton et al.*, 2007]. With this background, confidence in the model relies on testing whether or not its responses to these changes matches observed responses. In this paper, we made sensitivity analyses to environmental forcings using a model protocol that provided no site-specific constraints on the model apart from meteorology, N inputs and the predominant plant functional type. The intention of these analyses is not an in-depth evaluation of the model using the results of ecosystem manipulation experiments (this will be subject of forthcoming studies with O-CN), but to address the reliability of the model under contemporary conditions. Given this background, it is very encouraging that the response of O-CN to elevated CO<sub>2</sub> (from 288 ppmv in 1860 to 377 ppmv in 2000) matches qualitatively the effects observed in free air CO<sub>2</sub> enrichment experiments [e.g., *de Graaff et al.*, 2006; *Finzi et al.*, 2007], namely an increase in foliage area, a slight decline in foliage N concentrations, and a large increase in aboveground productivity. In response to elevated N inputs, most of the added N is sequestered in soil organic matter, which is in agreement with the <sup>15</sup>N tracer experiments of *Nadelhoffer et al.* [1999]. Increased N availability leads to increases in foliage N concentrations and foliage area, responses that are both observed in regions with high N deposition and in fertilizer experiments [*Linder and Murray*, 1998; *Karjalainen et al.*, 1999; *Hyvonen et al.*, 2007].

[44] The simulated gain in ecosystem C sequestration due to atmospheric N deposition averages 36 g C g<sup>-1</sup> N for the extended range of sites used in this study. This response varies substantially between sites, with values ranging from 2 to 79 g C g<sup>-1</sup> N depending on the initial soil N status and the magnitude of the increase in N deposition. These results are comparable to those obtained in ecosystem manipulation experiments with N addition rates within the range of current N deposition rates, i.e., when application rates are less than 50 kg N ha<sup>-1</sup> (mean: 36, range: 0–40 g C g<sup>-1</sup> N) [*Hyvonen et al.*, 2007], forest monitoring plots (25 g C g<sup>-1</sup> N) [*De Vries et al.*, 2006], and <sup>15</sup>N application studies in temperate forests (25 g C g<sup>-1</sup> N) [*Nadelhoffer et al.*, 1999]. However, the upper bound of the predicted range is much lower than the response of 175–225 g C g<sup>-1</sup> N suggested by analysis of the residual net ecosystem production once the effect of stand age on the net carbon flux is accounted for to make O-CN's estimates consistent with the observations [*Magnani et al.*, 2007, 2008]. A recent reanalysis of these same observations, as well as predictions by 3 site-scale forest growth models, suggests that the effect is actually around 50–70 g C g<sup>-1</sup> N [*Sutton et al.*, 2008]. The reason for the difference between these observational estimates and our simulations is likely related to the incomplete accounting in the simulations for co-occurring changes in climatic variables, as noted already by *Sutton et al.* [2008]. Accounting for the concurrent changes in climate and atmospheric CO<sub>2</sub> concentrations approximately doubles the responsiveness of NEP simulated by O-CN to an apparent 84 (50% confidence range: 60–170) g C g N<sup>-1</sup>, but including the mean estimate of *Magnani et al.* [2008] in higher quantiles (Figure 7b). Our model result highlights the importance of a mechanistic understanding of the processes

controlling the effects of N deposition, atmospheric CO<sub>2</sub> increase, and climate variation on the terrestrial C balance.

### 4.3. Comparison to Comparable Modeling Approaches and Outlook

[45] We have shown that O-CN produces realistic N and C flux and storage estimates and conclude that its performance is comparable to similar modeling approaches [e.g., *Raich et al.*, 1991; *McGuire et al.*, 1992; *Friend et al.*, 1997; *Thornton et al.*, 2002; *Xu-Ri and Prentice*, 2008]. The evaluation goes further than most model assessments in using eddy covariance data to evaluate diurnal and seasonal cycles of C fluxes, and by demonstrating a realistic simulation dynamic foliage N concentrations, and stand level nitrogen use efficiency. O-CN is a significant functional advance over the preceding version of ORCHIDEE [*Krinner et al.*, 2005], providing a process-based framework for simulating N effects on plant productivity and structure, and thereby terrestrial biogeophysics and biogeochemistry. It enables a more comprehensive simulation of the responses of terrestrial biosphere dynamics and accounts for N limitation and N deposition effects on terrestrial carbon and water exchanges. The new model provides a range of advances over existing C-N cycle models designed to assess global-scale consequences of terrestrial N feedbacks and their anthropogenic perturbations on terrestrial biogeochemistry [*Woodward et al.*, 1995; *Friend et al.*, 1997; *Dickinson et al.*, 2002; *Churkina et al.*, 2007; *Thornton et al.*, 2007; *Xu-Ri and Prentice*, 2008]. It achieves this by combining and extending, the following existing modeling approaches within a common modeling framework: N concentrations in vegetation and soil are flexible, directly affecting photosynthesis, autotrophic respiration, and soil organic matter decomposition rates; plant structure and, in particular, maximum annual foliage area, are sensitive to N availability; and all key N inputs and outputs are considered in a process-based manner at a half-hourly time scale.

[46] The model evaluations presented here are the first essential step toward the application of the joint carbon and nitrogen cycle land surface model O-CN in assessing the global importance of N cycling for the terrestrial C balance. In an accompanying manuscript [*Zaehle et al.*, 2010a], we apply the model globally over the historical period, and assess simulated regional and global carbon and nitrogen fluxes using in situ observations, remotely sensed data products, and atmospheric observations. The primary aim of O-CN is the study of land-atmosphere interactions, and *Zaehle et al.* [2010b] assess the performance of the model under the conditions of ecosystem manipulation experiments such as free air carbon dioxide enrichment and soil warming.

## 5. Conclusions

[47] The new version of the land surface scheme, O-CN, coupling terrestrial energy, water, carbon, and nitrogen processes in a globally applicable process-based modeling framework simulates realistic ranges of N tissue concentrations, N fluxes, and N turnover rates at a range of European temperate and boreal sites. The new model compares well with eddy covariance-based measurements

of diurnal and seasonal cycles of CO<sub>2</sub> fluxes to an extent similar to, or better than the same model framework but assuming no effects of N dynamics. Model results are reasonably robust with respect to the value of parameters used to scale process formulations. The results of the model evaluation presented here suggest that the coupling of terrestrial N dynamics to O-CN's energy, water, and carbon balances is of sufficient quality to merit testing at regional to global scales. Such an evaluation is given in an accompanying paper [Zaehle et al., 2010a].

[48] O-CN predicts realistic dynamics of soil N storage, foliage N concentrations, and foliage area to atmospheric N deposition relationships. The simulated response of the carbon balance of temperate and boreal forest ecosystems to N deposition ranges from 2 to 79 g C g<sup>-1</sup> N with a mean response of 36 g C g<sup>-1</sup> N. These results underline that while increased N deposition may contribute to terrestrial C sequestration, the effect is likely much less than suggested recently by Magnani et al. [2007], because of the confounding effect of concurrent changes in climate and atmospheric CO<sub>2</sub> concentrations. We investigate the regional and global consequences of changes in N deposition, climate, and atmospheric CO<sub>2</sub> concentration for historical and future terrestrial productivity and C sequestration in an accompanying paper [Zaehle et al., 2010a].

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