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Synergy of rising nitrogen depositions and atmospheric CO₂ on land carbon uptake moderately offsets global warming

Galina Churkina,^{1,2} Victor Brovkin,^{3,4} Werner von Bloh,³ Kristina Trusilova,¹ Martin Jung,¹ and Frank Dentener⁵

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[1] Increased carbon uptake of land in response to elevated atmospheric CO₂ concentration and nitrogen deposition could slow down the rate of CO₂ increase and facilitate climate change mitigation. Using a coupled model of climate, ocean, and land biogeochemistry, we show that atmospheric nitrogen deposition and atmospheric CO₂ have a strong synergistic effect on the carbon uptake of land. Our best estimate of the global land carbon uptake in the 1990s is 1.34 PgC/yr. The synergistic effect could explain 47% of this carbon uptake, which is higher than either the effect of increasing nitrogen deposition (29%) or CO₂ fertilization (24%). By 2030, rising carbon uptake on land has a potential to reduce atmospheric CO₂ concentration by about 41 ppm out of which 16 ppm reduction would come from the synergetic response of land to the CO₂ and nitrogen fertilization effects. The strength of the synergy depends largely on the cooccurrence of high nitrogen deposition regions with nonagricultural ecosystems. Our study suggests that reforestation and sensible ecosystem management in industrialized regions may have larger potential for climate change mitigation than anticipated.

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1. Introduction

[2] Burning of fossil fuel and land use change release carbon dioxide (CO₂), which is the most important greenhouse gas with a radiative forcing of about 1.66 W/m². If carbon uptake of the land or ocean weakens in the future, atmospheric CO₂ concentrations increase even faster [Raupach *et al.*, 2007]. Future trajectories of atmospheric CO₂ concentrations depend on the land responses to changing climate as well as to simultaneous rising of atmospheric CO₂ and nitrogen deposition, which both can increase plant growth [DeLucia *et al.*, 2005; Finzi *et al.*, 2007] and soil respiration [King *et al.*, 2004]. Although regional climate changes can have both positive and negative effects on carbon uptake, recent modeling studies point to reduction of global land uptake in the future primarily because plant and soil respiration increase with elevated temperatures [Friedlingstein *et al.*, 2006]. Physiological effect of elevated atmospheric CO₂ on plant productivity is considered to offset the negative effect of climate and is debatably used to explain an increase in the global carbon uptake of land in

the end of last century. Model simulations [Cramer *et al.*, 2001] suggest net global carbon uptake of 2.4 PgC/yr in 1990s due to the CO₂ fertilization effect alone. This study assumes that productivity of land ecosystems is not limited by nitrogen availability. Nitrogen is however reported to be a primary limiting nutrient throughout terrestrial ecosystems of mid and high latitudes, and an important limiting nutrient for plant growth throughout subtropical and tropical ecosystems [Vitousek *et al.*, 1998], where phosphorus is a colimiting or limiting nutrient [D'Antonio and Mack, 2006; Tanner *et al.*, 1998]. Recent findings from field studies [Reich *et al.*, 2006] point to nitrogen availability being a constraint to CO₂-induced stimulation of plant growth. Low availability of nitrogen in the soils appears to suppress the positive response of plant growth to elevated CO₂. Anthropogenic increase in nitrogen deposition enhances availability of nitrogen in soil and this increase has been shown to correlate with the sequestration of carbon by the European forests [Magnani *et al.*, 2007]. Although the amount of reactive nitrogen globally has doubled between 1860 and 1990s [Galloway *et al.*, 2004], continues to increase, and is mostly deposited on land, it is still far from being plentiful nutrient for land ecosystems [Hungate *et al.*, 2003], which are usually nitrogen limited [Vitousek *et al.*, 2002]. It is a matter of debate how land ecosystems respond to simultaneously changing climate, rising atmospheric CO₂, and nitrogen deposition.

[3] A number of global scale studies addressed the responses of land ecosystems to rising nitrogen deposition

¹Max Planck Institute for Biogeochemistry, Jena, Germany.

²Leibniz Centre for Agricultural Landscape Research, Müncheberg, Germany.

³Potsdam Institute for Climate Impact Research, Potsdam, Germany.

⁴Max Planck Institute for Meteorology, Hamburg, Germany.

⁵Joint Research Centre, Institute for Environment and Sustainability, European Commission, Ispra, Italy.

during the last few decades. Based on results from a series of ¹⁵N-tracer field experiments, *Nadelhoffer et al.* [1999] argued that increased inputs of nitrogen from the atmosphere made a minor contribution to land carbon uptake with an additional 0.25 PgC per year being sequestered. In contrast, model based estimates [*Holland et al.*, 1997; *Townsend et al.*, 1996] showed significant increases in land carbon uptake. Using the ecosystem model CENTURY and various predicted spatial distributions of atmospheric nitrogen deposition, *Holland et al.* [1997] estimated carbon uptake of 1.5–2.0 Pg per year induced by nitrogen deposition. The most recent study with the BIOME-BGC model [*Churkina et al.*, 2007] showed that elevated nitrogen deposition would not significantly enhance land carbon uptake unless effects on regrowing forests are considered. They reported that nitrogen enriched land ecosystems sequestered 0.75–2.21 PgC in the 1990s depending on the proportion and age of regrowing forests. *Thornton et al.* [2007] investigated the importance of carbon-nitrogen interactions on land for the climate system. They pointed out that including carbon-nitrogen interactions in the land carbon model substantially changes dynamics of several critical feedbacks between land and climate system. For instance, the sensitivity of land carbon fluxes to changing temperature and precipitation decreases with rising atmospheric CO₂. The question to what extent nitrogen deposition has potential to slow down the atmospheric CO₂ increase and thus to mitigate climate change remains open.

[4] We use a coupled model of climate, ocean, and land biogeochemistry to investigate feedbacks between increasing atmospheric nitrogen depositions, land ecosystems, atmospheric CO₂, and climate. First we isolate the contributions of transient changes in climate, atmospheric CO₂, and nitrogen deposition to the net carbon flux variability of land from 1860 to 2030. We also investigate how this impacts concentration of CO₂ in the atmosphere and global temperature.

2. Methods

2.1. Coupled System

[5] To investigate feedbacks between climate, atmospheric CO₂, atmospheric nitrogen deposition and carbon uptake of the land over almost two centuries, we coupled an earth system model of intermediate complexity, CLIMBER-2 with a biogeochemical process model BIOME-BGC.

2.1.1. CLIMBER-2 Description

[6] CLIMBER-2 [*Petoukhov et al.*, 2000] comprises a 2.5-dimensional dynamical-statistical atmosphere model (10° latitude and 51° longitude), a 3-basin, zonally averaged ocean model (latitudinal resolution 2.5°), a sea-ice model, a terrestrial vegetation model (used here for parameterization of biophysical processes of land surface – atmosphere exchange), and a model of oceanic biogeochemistry [*Brovkin et al.*, 2002]. CLIMBER-2 is able to reproduce present-day and paleoclimates [*Claussen et al.*, 1999] and compares well with complex climate system models [*Ganopolski et al.*, 2001].

2.1.2. BIOME-BGC Description

[7] The terrestrial biogeochemical model BIOME-BGC [*Running and Hunt*, 1993; *Thornton*, 1998] calculates water,

carbon, and nitrogen pools as well as their fluxes on a daily basis. The model is able to reproduce carbon and water fluxes, stem increments, and other components of the carbon cycle for a range of ecosystems [*Churkina and Running*, 2000; *Cienciala et al.*, 1998; *Thornton et al.*, 2002; *Vetter et al.*, 2005]. BIOME-BGC is also able to replicate responses in net carbon exchange of forest ecosystems to different levels of atmospheric nitrogen deposition [*Churkina et al.*, 2003]. The model is forced by maximum and minimum surface daily air temperature, precipitation, air humidity, and solar radiation data. Carbon dynamics include calculations of the plant photosynthesis, growth, allocation of assimilates to the different plant organs, mortality as well as litter and soil organic matter decomposition. Plant demand for nitrogen is calculated from potential gross primary productivity and carbon to nitrogen ratios of plant organs. Demand of soil microbial community for nitrogen is determined by potential litter and soil organic matter available for decomposition and carbon to nitrogen ratios of corresponding pools. The amount of nitrogen available to satisfy this demand is computed as the sum of nitrogen deposited from atmosphere, biological fixation, and nitrogen mineralized from soil organic matter decomposition. Soil microbial community has a priority in getting mineralized nitrogen. If the demand for nitrogen of the plant or the soil is not met, the potential gross primary productivity and soil decomposition are reduced accordingly. Therefore, the model is able to reproduce direct feedbacks between nitrogen availability and biomass growth or soil decomposition. Nitrogen loss from ecosystem includes leaching of nitrogen with water outflow and gaseous losses during fire. Volatilization of nitrogen from soil mineral nitrogen pool is not explicitly calculated, because global scale controls over denitrification are still under development [*Kulkarni et al.*, 2008]. Nitrogen leaching from ecosystem is determined by the amount of soluble mineral nitrogen available, water outflow, and soil water content. Detailed description of nitrogen cycle can be found elsewhere [*Thornton*, 1998]. Possible forest dieback subjected to high nitrogen inputs was not considered in this study, because the atmospheric nitrogen depositions were averaged over relatively coarse grid cells and did not reach the high values, which could cause nutritional imbalance of forests.

2.1.3. BIOME-BGC Parameterization and Initialization

[8] The model (version 4.1.1 with carbon and nitrogen allocation routine from 4.1) was parameterized for seven vegetation types such as deciduous broadleaf forest, evergreen needleleaf forest, evergreen broadleaf forest, evergreen deciduous forest, shrubland, C4 and C3 grasslands. Parameters for evergreen needleleaf and deciduous broadleaf forests (e.g., carbon to nitrogen ratios of forest ecosystem's pools) were optimized from field measurements of net carbon fluxes [*Trusilova et al.*, 2009]. Parameterizations for evergreen broadleaf forest, deciduous needleleaf forest, shrublands, C3 and C4 grasslands were from *White et al.* [2000].

[9] All input data were transformed to a 1° × 1° spatial resolution and subsequent spatially explicit simulations with the BIOME-BGC model were performed at this spatial resolution as well. Input land surface characteristics includ-

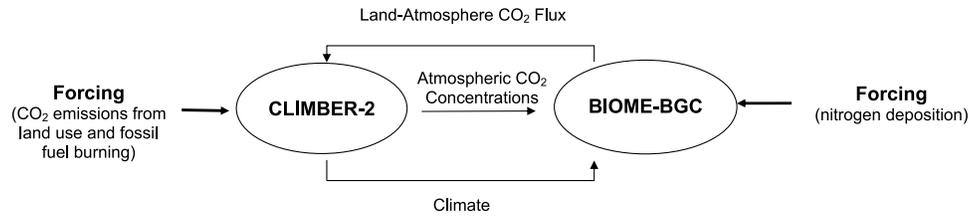


Figure 1. Coupled modeling system used for simulations in this study.

ed digital elevation map, soil texture map, and land cover classification.

[10] Carbon and nitrogen state variables of the BIOME-BGC model represent amounts of carbon and nitrogen stored in simulated plant and soil pools. State variables can be initialized either from measurements or from model simulations (spin-up run). In the spin-up run, the model is run to a steady state to obtain the size of the ecosystem's carbon and nitrogen pools under the assumption of ecosystem being in equilibrium with the long-term climate. Since measured values for model's state variables globally are not available, model simulations were performed for their initialization in this study. The model spin-up simulation was performed with daily climate data from NCEP Reanalysis [Kalnay *et al.*, 1996] for 1968–1977, constant preindustrial atmospheric nitrogen deposition (0.0002 kgN/m²/yr) and CO₂ concentration (286 ppm).

2.2. Estimation of Atmospheric CO₂ in a Coupled System

[11] Atmospheric CO₂ concentrations are modified by CO₂ fluxes from ocean and land. In this study the change in atmospheric CO₂ was resolved on an annual time step as:

$$C_A(t+1) = C_A(t) + \beta^* \{E(t) + F_{OA}(t) + F_{LA}(t, C_A(t-1))\}, \quad (1)$$

where C_A is atmospheric CO₂ concentration (ppmv), β is a conversion factor (0.47 ppmv/Pg C) from units of carbon to units of CO₂, E is anthropogenic CO₂ emissions (Pg C/yr), F_{OA} and F_{LA} are annual ocean-atmosphere and land-atmosphere net carbon fluxes (PgC/yr), respectively.

[12] The CLIMBER-2 model was used for the calculation of atmospheric CO₂ concentration (equation (1)) and climate anomalies that were passed to BIOME-BGC (Figure 1). Anthropogenic CO₂ emissions (E) for years 1860–2000 and for the IPCC SRES A2 scenario for the period 2000–2030 were obtained from the recent C4MIP intercomparison study [Friedlingstein *et al.*, 2006]. Anthropogenic emissions included CO₂ fluxes from fossil fuel burning and land use change (except one sensitivity simulation which did not include the land use emissions). Carbon fluxes resulting from photosynthesis and respiration of land ecosystem were estimated with the BIOME-BGC model each year, while annual carbon fluxes from the ocean (F_{OA}) were modeled by CLIMBER-2. The atmospheric CO₂ (C_A) calculated in accordance with equation (1) was used as an input for BIOME-BGC in calculating F_{LA} for the next year, thus creating the biogeochemical feedback between CLIMBER-2 and BIOME-BGC. CLIMBER-2 provided BIOME-BGC

with monthly anomalies of surface air temperature, precipitation, and downward shortwave radiation. These anomalies were computed as differences between corresponding climate variables in the current year of the transient run and the year 1860 (initial simulation year). The climate simulated by CLIMBER-2 responded to atmospheric CO₂ increase. Biogeochemical and hydrological processes within BIOME-BGC were forced by simulated trend in climate obtained from CLIMBER-2. The climate anomalies from CLIMBER were added to the daily climatology for one year which was randomly selected from the NCEP Reanalysis data [Kalnay *et al.*, 1996] for the years 1948–1952. We chose climate data for the earliest part of the reanalysis period, when climate was least affected by anthropogenic change. Absolute climate anomalies were used for temperature and radiation. Relative climate anomalies were used for precipitation because absolute values of precipitation simulated by climate models are often biased. The modified climate variables were used to drive simulations of the BIOME-BGC model for the next year, thus generating a climatic feedback between CLIMBER-2 and BIOME-BGC. Radiative forcings of other greenhouse gases such as CH₄ and N₂O, as well as of sulphate aerosols were neglected.

2.3. Model Simulations

[13] To evaluate effects of different factors on land carbon uptake and consequently on atmospheric CO₂, we performed seven simulations (Table 1) of the coupled model from 1860 to 2030. The atmospheric CO₂ and ocean carbon cycle were interactive in all runs. In the control simulation (Control), CLIMBER-2 atmosphere and ocean model were interactive with rising CO₂ concentrations driven by emissions from fossil fuel burning and land use change. The BIOME-BGC model was driven by daily NCEP Reanalysis climate values for 1948–52, with years randomly shuffled, constant CO₂ concentrations (286 ppm) and nitrogen deposition (0.0002 kgN/m²/yr) as in spin-up simulation. The control simulation represents the state of biosphere undisturbed by climate change, CO₂ and nitrogen fertilization. We isolated and combined the effects of climate change, elevated CO₂, and nitrogen deposition by simulations with climate change only (Clim), with CO₂ increase but no climate change and no nitrogen deposition increase (CO₂), and with nitrogen deposition increase but no climate change and no CO₂ increase (N_{high}). Three model simulations (Clim + CO₂ + N_{high}, Clim + CO₂ + N_{low}, and Clim + CO₂ + N_{high}-LU), were performed with all factors changing. Simulation “Clim + CO₂ + N_{low}” was performed with low nitrogen deposition from IASA maximum feasible reduction scenario 2030 [Dentener *et al.*, 2006]. The “Clim + CO₂ + N_{high}” simula-

Table 1. Protocol of Simulations Performed With the Coupled Model for 1860–2030^a

Simulation	Climate Change	Fossil Fuel Emissions	Land Use Emissions	Nitrogen Deposition Change
Control	No	No	Yes	No
Clim	Yes	No	Yes	No
CO ₂	No	Yes	Yes	No
N _{high}	No	No	Yes	SRES A2 2030
Clim + CO ₂ + N _{high}	Yes	Yes	Yes	As above
Clim + CO ₂ + N _{high} -LU	Yes	Yes	No	As above
Clim + CO ₂ + N _{low}	Yes	Yes	Yes	IIASA maximum feasible reduction scenario 2030

^aEmissions of CO₂ from fossil fuel burning and land use change for years 1860–2000 and the climate IPCC SRES A2 scenario for the period 2000–2030 were obtained from the recent C4MIP intercomparison study [Friedlingstein *et al.*, 2006]. Nitrogen deposition was estimated with TM3 [Rodhe *et al.*, 2002] for 1860–1980 and with the mean of an ensemble of model results for 2000 and 2030 [Dentener *et al.*, 2006].

tion was executed with high nitrogen deposition from SRES A2 2030 scenario [Dentener *et al.*, 2006] and with CO₂ emissions from land cover conversion. To estimate the effect of CO₂ emissions from land use change on temperature and atmospheric CO₂ we also performed model simulation with high nitrogen deposition and no emissions from land use (LU) change (Clim + CO₂ + N_{high}-LU). Because land cover conversion is not simulated with the current version of the BIOME-BGC model, carbon flux from land use change has been prescribed in this simulation from [Friedlingstein *et al.*, 2006].

[14] All above mentioned simulations were first performed with potential (described below) and then with present vegetation (SYNMAP) [Jung *et al.*, 2006]. In simulation with present vegetation, net carbon balance of croplands was assumed to be close to neutral given that their biomass is regularly harvested. Although we assume no changes in vegetation cover in all simulations, we account for carbon emissions from land use change when calculating atmospheric CO₂ as described above.

[15] A new potential vegetation map optimized for BIOME-BGC vegetation classes and compatible with the present vegetation map [Jung *et al.*, 2006] was constructed (see Text S1).¹ This map is based on adaptive filtering of anthropogenic classes such as urban and cropland with replacement of the majority class of natural vegetation using several high resolution (1km) land cover products. The advantages of this potential vegetation map is that it is based on an advanced reproduction method (more recent data sets and advanced filtering approach than other maps) and is optimized for applications with carbon cycle models.

2.3.1. Climate Change

[16] Climate anomalies were calculated by CLIMBER-2 and imposed over daily NCEP Reanalysis climate values for 1948–52 as described above. The BIOME-BGC simulations were driven by these modified climate values at a daily time step.

2.3.2. Atmospheric CO₂ Change

[17] In the year 1860, atmospheric CO₂ concentration was prescribed to 286 ppmv in accordance with ice core data [Etheridge *et al.*, 1996]. Hereafter, atmospheric CO₂ dynamics were calculated interactively by the coupled modeling system as described above (equation (1)) and used to drive simulations of the BIOME-BGC model in all simulations except the ones with fixed CO₂.

2.3.3. Nitrogen Deposition Change

[18] State-of-the-art atmospheric nitrogen deposition estimates for 1860–2030 were used to drive simulations of BIOME-BGC (Figure 2). The spatial distribution of atmospheric nitrogen deposition was estimated with the three dimensional atmospheric chemical transport model TM3 [Rodhe *et al.*, 2002] for 1860–1980 and with the mean of an ensemble of model results [Dentener *et al.*, 2006] for 2000 and 2030. The estimates included wet and dry depositions of both NO_y and NH_x. The depositions of reactive nitrogen in 2030 were estimated with two scenarios: (1) a “low emission” scenario assuming maximum emission reduction that is currently technologically feasible; (2) a “high emission” scenario which corresponds to the IPCC SRES A2 scenario. The original decadal model outputs for 1860–1980 as well as for 2000 and 2030 were transformed into time series of annual atmospheric nitrogen depositions using linear interpolation for each grid pixel.

[19] To analyze the relative contributions of rising atmospheric CO₂ and nitrogen deposition to the land carbon uptake we calculated the difference of the global carbon balance of the respective scenario and of the control run for the 1990s. The relative contributions were given as percent change of the net carbon flux.

3. Results and Discussion

3.1. Responses of Land Ecosystems

3.1.1. Corroboration

[20] Our global and continental scale estimates of land carbon uptake in 1990s are consistent with previously reported data. Our best estimate of global land carbon uptake is 1.34 PgC/yr for 1990s. This estimate is a result from model simulations for present vegetation cover with all factors included (Clim + CO₂ + N_{high}). Our best estimate is within the uncertainty range of the uptake reported recently for 1990s 0.9 to 4.3 PgC (best estimate: 2.6 PgC) [Solomon *et al.*, 2007]. We estimate the carbon uptake of geographic Europe at 0.08 PgC/yr, which is comparable to the previous estimate of 0.11 ± 0.28 PgC/yr from the analysis of different land-based approaches [Janssens *et al.*, 2003]. The North American ecosystems sequester around 0.23 PgC/yr according to our model simulations that is also within the uncertainty range of recent estimate 0.5 ± 0.25 PgC/yr from a variety of sources [King *et al.*, 2007]. Our estimates of land carbon fluxes are on the low side because no land management or forest age effects were included in our model simulations, but in the other estimates they were. In addition

¹Auxiliary materials are available in the HTML. doi:10.1029/2008GB003291.

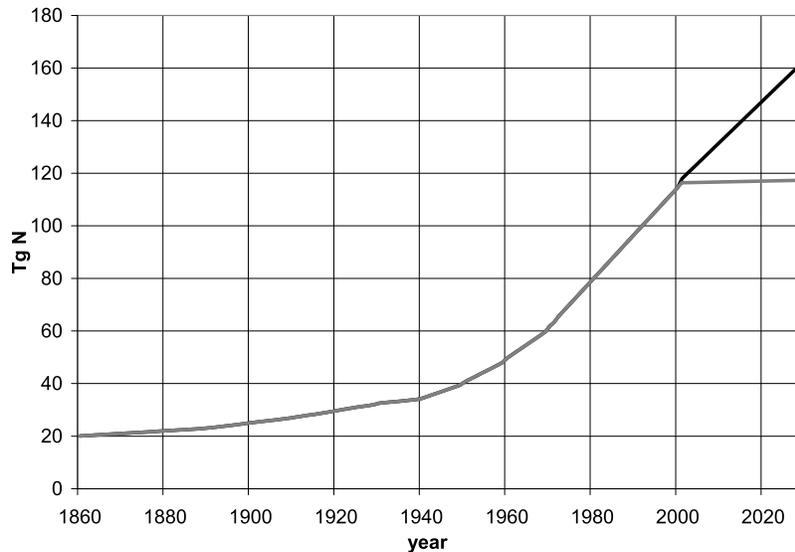


Figure 2. The global atmospheric nitrogen deposition for 1860–2030 used in the model simulations. Two scenarios with high (black line, SRES A2 2030) [Dentener *et al.*, 2006] and low (gray line, IIASA Maximum feasible reduction scenario 2030) [Dentener *et al.*, 2006] nitrogen depositions are displayed. Two scenarios coincide for 1960–2000. The estimates include wet and dry depositions of both NO_x and NH_x.

areas dominated by croplands were excluded from these calculations.

[21] Although a direct validation of the responses of modeled NPP to nitrogen deposition and elevated CO₂ is desirable, it remains problematic because of the differences in experimental designs of field and model experiments. Soil nitrogen status, frequency and intensity of nitrogen additions play important roles in the ecosystem's response to it. Frequency and magnitude of nitrogen addition in the field (1–2 times per year, 1–1000 kgN/ha/yr) cannot be directly compared to the continuing nitrogen deposition from atmosphere (2–45 kgN/ha/yr) in our numerical simulations. Moreover, the atmospheric nitrogen deposition is already included as a background deposition in addition to the nitrogen fertilizers in the control experimental studies. The modeled global NPP increase (on average 4% in 1990s) is lower than the results of recent meta-analyses of nitrogen addition experiments, but not unreasonable given the differences on experimental designs of field and model experiments. Aboveground NPP was increased by approximately 28–29% in the cross-biome analyses of terrestrial plants [Elser *et al.*, 2007; LeBauer and Treseder, 2008]. The average biomass response to low nitrogen addition amounts (approx. 10–50 kgN/ha/yr) was 24.6% for woody and 50% for herbaceous plants [Xia and Wan, 2008]. The modeled response of global NPP to elevated CO₂ (8% increase at 560 ppm of CO₂) is also lower than the response of the dry matter production reported in field studies, which ranges from 10% for C3 grasses to 28% for forests at 550–600 ppm of CO₂ [Ainsworth and Long, 2005]. Trees grown under nutrient limitations however had a nonsignificant 14% stimulation in aboveground biomass [Ainsworth and Long, 2005]. Again ecosystems can have different responses to CO₂ continuously rising over 130 years in modeling exper-

iment and to high CO₂ levels kept at a constant level for 6–10 years in field experiments. Some field studies suggest that plant growth response to elevated CO₂ slows over time, likely due to reduced nitrogen availability [Hungate *et al.*, 2006].

[22] In addition to differences in experimental designs, changes in allocation patterns of ecosystems in CO₂ and nitrogen enrichment experiments [Finzi *et al.*, 2006a; Finzi *et al.*, 2006b; Gill *et al.*, 2006; Norby and Iversen, 2006] may be responsible for discrepancies between model and experimental results. The allocation pattern change has not been accounted for in the BIOME-BGC model, because mechanisms behind the different and sometimes contrasting allocation responses of ecosystems are still poorly understood.

3.1.2. Attribution

[23] The dominant anthropogenic driver of net ecosystem productivity (NEP) shifts in the model over 170 years (Figure 3). Before 1990 NEP increases more in response to elevated atmospheric CO₂ than to rising nitrogen deposition. Starting in the 1990s, the effect of nitrogen deposition overtakes the fertilization effect of rising CO₂ on net carbon uptake. By 2030 the global NEP driven by increasing nitrogen deposition is higher than NEP driven by rising CO₂, which saturates at 0.3 PgC/yr. Global gross primary productivity (GPP) of land ecosystems in response to elevated CO₂ does not saturate although NEP (Figure 4) and net primary productivity (NPP, not shown) do. GPP driven by rising CO₂ is higher than GPP driven by rising deposition of nitrogen until 2020. Global modeled NPP in response to elevated CO₂ slows down over time similar to growth responses of plants [Hungate *et al.*, 2006], due to reduced nitrogen availability. The saturation in NEP response to elevated atmospheric CO₂ in the “CO₂” only

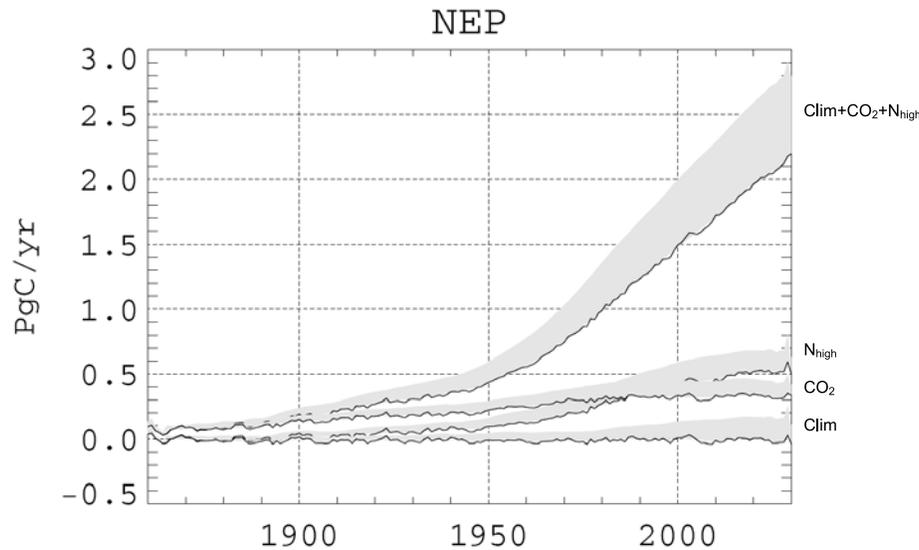


Figure 3. Effects of increasing atmospheric CO₂ and nitrogen deposition on net carbon flux from land. Shaded area shows effect of vegetation on NEP response. The upper bound of the shaded area was simulated with potential vegetation cover. The lower bound (black solid line) was simulated with present vegetation cover and crops assumed to be carbon neutral. NEP is steadily increasing in scenarios with rising nitrogen deposition only and in with all factors changing.

simulation is related to respiration which increases at rates comparable with GPP after 1990s.

[24] The effect of changing climate on net carbon fluxes of land is almost negligible (Figure 3), because GPP (Figure 4) and respiration (not shown) are increasing at similar rates. In simulations with potential vegetation changing climate leads to a slight increase of NEP (0.1 PgC/yr in the 1990s), which indicates that GPP increase is higher than respiration rise. In

the case of potential vegetation the area of nitrogen limited forests is more extensive. Rising temperatures enhance decomposition of forest soil and release more inorganic nitrogen reducing nitrogen limitation of forest carbon uptake which overcompensates the respiration loss.

3.1.3. Synergistic Effect

[25] Our model simulations suggest a considerable synergistic or nonadditive effect of increasing atmospheric CO₂

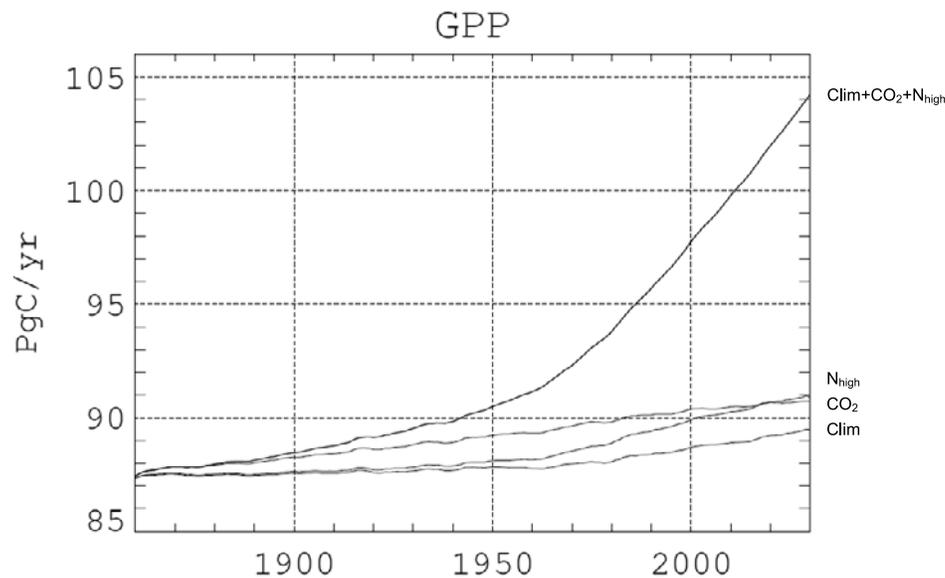


Figure 4. Effects of increasing atmospheric CO₂ and nitrogen deposition on GPP of land ecosystems. GPP was simulated with present vegetation cover and crops assumed to be carbon neutral. After 1990s, GPP continues to increase in scenario with increasing CO₂ only, even though NEP levels off.

Table 2. Relative Contributions of Elevated Atmospheric CO₂, Nitrogen Deposition, Climate, and Combined Effect of All Factors on Modeled GPP, NPP, and NEP of Land Ecosystems^a

Factors Affecting Land Carbon Fluxes	Global GPP (%)	Global NPP (%)	Global NEP (%)	European NEP (%)	North American NEP (%)
CO ₂ , climate and N deposition	100	100	100	100	100
N deposition	23	35	28.7	39.7	21.7
CO ₂	30	29	24.2	19.3	26.5
Climate	11	7	-0.2	-3.6	-1.7
Synergistic	36	28	47.3	44.6	53.5

^aEach relative contribution is given as a percent change of the respective annual carbon flux averaged for the 1990s. All values were calculated in four model simulations (CO₂, N_{high}, Clim, and Clim + CO₂ + N_{high}) with present vegetation cover. The fertilization effects of atmospheric CO₂ and nitrogen deposition on NEP are nonadditive.

and nitrogen deposition on global NEP, GPP, and NPP (Table 2). In the 1990s the global synergistic effect for NEP is about 47%, which is higher than either the effect of increasing nitrogen deposition (29%) or CO₂ fertilization (24%). The synergistic effect for GPP and NPP (36% and 28% respectively) are lower than for NEP. Synergy implies that the net effect of both atmospheric CO₂ and nitrogen deposition on NEP is higher than a sum of effects of each forcing taken separately. The synergistic (nonlinear) effect can be observed in the ecosystems colimited by several factors such as climate, CO₂ and nitrogen availability. When these limitations on ecosystem productivity simultaneously release, one can observe synergistic effect [Henry *et al.*, 2006; Oren *et al.*, 2001]. The simultaneous release of a few limitations does not always have a synergistic effect in a model. The effect will be additive if a productivity is calculated as a sum of functions of independent variables. The effect will be synergistic if productivity is a complex nonlinear function of independent variables, which is the case in the BIOME-BGC model, G'DAY model [Pepper *et al.*, 2005] and in a model by Lloyd [1999]. In contrast, effects of different treatments are additive in DAYCENT [Pepper *et al.*, 2005].

[26] In our study the synergy represents effects averaged over different ecosystems and climate conditions. In previous field and modeling studies the synergistic effect was reported for single ecosystems and is slightly lower than our results. In field studies the synergistic effect of CO₂ and nitrogen fertilization was about 25% for woody tissues increment of needleleaf forest [Oren *et al.*, 2001], which is consistent with our simulated 28% NPP increase. In a modeling study the synergistic effect for net ecosystem productivity of a deciduous forest was between 34 and 43% increasing with higher nitrogen deposition loads [Lloyd, 1999]. Recent experimental study of grassland by Henry *et al.* [2006] points to the complexity of interactions between CO₂, nitrogen additions, soil moisture and burning effects on the productivity. In unburned plots they found no interactive effects of elevated CO₂ and nitrate additions on plant productivity. However, fire can substantially modify responses of ecosystems to CO₂ and nitrate additions.

[27] In model simulations with present vegetation, the synergistic effect is slightly lower in Europe than in North America. It amounts to 45% and 53% respectively for present vegetation (Table 2). The CO₂ fertilization has also a lower impact on carbon uptake in Europe (19%) than in North America (26%). In opposite, the rising nitrogen deposition enhances the carbon uptake of Europe more

(40%) than the carbon uptake of North America (22%). A greater sensitivity of North American ecosystems to CO₂ fertilization effect can be explained by a relatively high proportion of grasslands and shrublands (43% of land area), which are mostly water limited [Churkina and Running, 1998] and are sensitive to CO₂ fertilization effect. European ecosystems are limited mostly by radiation and temperature, therefore their response to increase in atmospheric CO₂ is lower. In Europe nitrogen deposition has a higher fertilization effect on land ecosystems than in North America, because more nitrogen-limited ecosystems, such as forests, are exposed to high deposition of reactive nitrogen. Increased nitrogen deposition was recently shown to correlate with carbon uptake of European forests [Magnani *et al.*, 2007].

3.1.4. Spatial Patterns

[28] We found that largest changes in simulated carbon uptake on land have happened in industrial regions such as Eastern North America, Europe, and South East Asia (Figures 5a and 5b), where nitrogen emissions and deposition are the highest. In 2030 areas with carbon uptake increase higher than 0.2 kgC/m² per year cover not only "old" industrial regions (Europe, North America and South East Asia) but also "emerging" industrial regions (Africa and South America). In 2030, the increase in annual carbon uptake reaches 0.4 kgC/m² in South East Asia. The strength of land response to the combined effect of anthropogenic forcings and its implications for atmospheric CO₂ concentrations and global temperature is related to vegetation types and their distribution in the industrial regions. The strongest effect (Figure 5a) is obtained with potential vegetation, where large areas of Europe, North America, and Asia are covered by forests. Since forests have high carbon to nitrogen ratios and long lifetimes of carbon in wood, a most significant effect was obtained in forests. The result from simulations with present vegetation shows a considerably weaker response of land. The industrial regions have currently not only the highest nitrogen emission and deposition, but also large areas covered by managed ecosystems (e.g., croplands, pastures, urban sprawl) which already receive high fertilization additions and are mostly insensitive to environmental changes considered in the study [Ewert *et al.*, 2007]. Reforestation of the industrial regions however may increase the carbon uptake on land and its influence on the rising atmospheric CO₂, given the high sensitivity of the regrowing trees to synergistic effect [Churkina *et al.*, 2007].

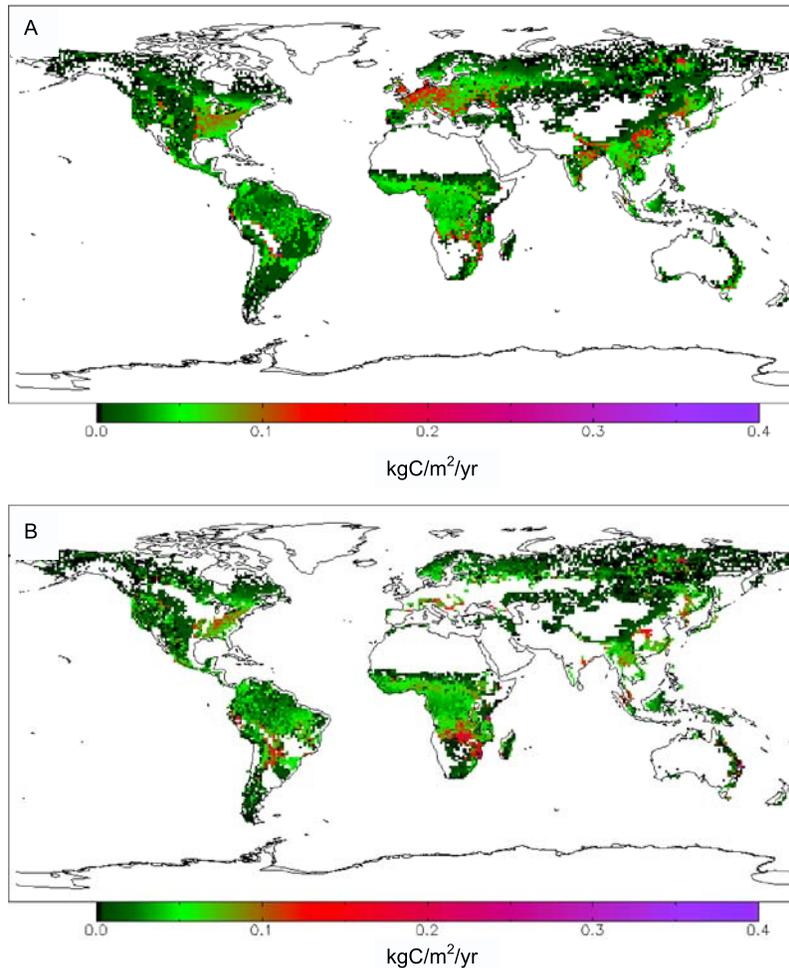


Figure 5. Changes in NEP in 2030 assuming rising atmospheric CO₂ and nitrogen deposition with (a) potential and (b) present vegetation cover. NEP value at each grid cell is calculated as a difference between annual NEP calculated with all factors changing (Clim + CO₂ + N_{high}) and annual NEP estimated with constant CO₂ and nitrogen deposition in 2030.

3.2. Responses of Atmospheric CO₂ and Global Temperature

[29] The differences in atmospheric CO₂ and temperature from simulations with high (Clim + CO₂ + N_{high}) and low (Clim + CO₂ + N_{low}) nitrogen deposition were not considerably different (Table 3). The two scenarios of nitrogen deposition were identical from 1860 until 2000. Thereafter nitrogen deposition globally was continuously increasing from 91.4 TgN/yr up to 139.1 TgN/yr in N_{high} scenario and up to 93.1 TgN/yr in N_{low} scenario. In 2030 the difference of 46 TgN/yr in nitrogen deposition resulted in only 2 ppm difference of atmospheric CO₂ and no difference in global temperature compared to the high nitrogen deposition scenario (Table 3). Henceforth we discuss only results from model simulations with high nitrogen deposition (N_{high}) because the conclusions for the model simulations with low nitrogen deposition would be similar.

[30] Our results suggest that rising atmospheric CO₂ and nitrogen deposition (Clim + CO₂ + N_{high}) can lead to an increase of carbon uptake on land and consequently to a measurable reduction in atmospheric CO₂ concentration. By

2030 all factors together (Clim + CO₂ + N_{high}) offset atmospheric CO₂ by 41 ppm in comparison to the control simulation (Table 4). Among all factors the synergetic response of land is responsible for the most significant offset of atmospheric CO₂, which is 16 ppm. Physiological

Table 3. Changes in Atmospheric CO₂ and Global Annual Temperatures From 1860 to 2030^a

Simulation	Atmospheric CO ₂ Increase (ppm)	Temperature Increase (°C)
Control	241	1.4
Clim + CO ₂ + N _{high}	200	1.2
Clim + CO ₂ + N _{low}	202	1.2
Clim + CO ₂ + N _{high} - LU	152	1.0
N _{high}	230	1.4
CO ₂	228	1.4
Clim	239	1.4

^aFor each model simulation the changes are calculated as the difference between simulated CO₂ concentrations or global mean temperatures in 1860 and 2030. Model simulations were performed with present vegetation cover.

Table 4. Contributions of Different Mechanisms Affecting Land Carbon Balance to Changes in Atmospheric CO₂ Concentrations^a

Factor Affecting Land NEP	Change in Atmospheric CO ₂ During 1860–2030 (ppmv)	Factor Contribution (%)
CO ₂ , climate and N deposition	–41	100
N deposition	–11	26
CO ₂	–13	30
Climate	–2	5
Synergistic	–16	38

^aCO₂ concentrations are obtained from four model simulations (CO₂, N_{high}, Clim, and Clim + CO₂ + N_{high}). Synergy is a nonlinear term in the full factor experiment.

fertilization effect of CO₂ on plants gives offset of 13 ppm and increasing nitrogen deposition on land ecosystems reduces atmospheric CO₂ by 11 ppm. The offset in atmospheric CO₂ is considerably higher (76 ppm in 2030) if potential vegetation cover is used in the model simulations.

[31] Global temperature shows a moderate response to the effect of increasing nitrogen deposition, rising CO₂, and changing climate, because we performed model simulations in this study over a relatively short period of time. By 2030, response of land reduces temperature by 0.2–0.4°C depending if emissions from land use change were included in the simulations with present vegetation or not (Table 3). Projections of both NO_y and NH_x depositions until 2100 would be desirable to investigate feedbacks between climate, carbon flux from nitrogen fertilized land ecosystems, and atmospheric CO₂ concentrations.

[32] Changes in climate from 1860 to 2030 do not play a significant role in net carbon uptake on land with present vegetation (Figure 3 and Table 2). Therefore, the difference in atmospheric CO₂ concentrations estimated with and without changes in climate (Clim and Control simulations)

is almost negligible. By 2030 the difference between results from these two simulations is –2 ppm (Table 3). Because our study is focused on land carbon response to anthropogenic forcing, we have not performed an analysis of oceanic CO₂-temperature feedback. This analysis would require an additional simulation without climate change effect on ocean biogeochemistry such as uncoupled simulation by *Friedlingstein et al.* [2006]. An effect of sea surface warming on oceanic CO₂ uptake (which results in a CO₂ release from the ocean) is accounted for in simulations with and without climate change.

[33] Increase in atmospheric CO₂ concentrations simulated with the coupled model in this study is comparable with observations (Figure 6). In 2000 observed concentrations are 9 ppm higher than CO₂ concentrations simulated without accounting for emissions from land use change (Climate + CO₂ + N_{high} - LU). Simulated atmospheric CO₂ concentration is 17 ppm higher than the atmospheric measurements once we include land use emissions in our calculations (Climate + CO₂ + N_{high}). These estimates of atmospheric CO₂ include three sources of uncertainty: emissions from land use change, fluxes from land ecosystems, and the ocean. The largest uncertainty here arises from estimates of emissions from land use change. Land use emissions we use are possibly overestimated [*Brovkin et al.*, 2004; *Jones et al.*, 2003]. The recent estimate of emissions from land-use change during 1990s was 1.6 PgC/yr [*Solomon et al.*, 2007], which is 40% less than emissions assumed in our scenario. Also uncertainties in the estimated ocean carbon sink can contribute to the discrepancy between modeled and observed atmospheric CO₂ concentrations. Ocean uptake in the (Climate + CO₂ + N_{high}) simulation was 2.0 PgC/yr during 1990s, which is slightly lower than the recent estimate of 2.2 PgC/yr [*Solomon et al.*, 2007].

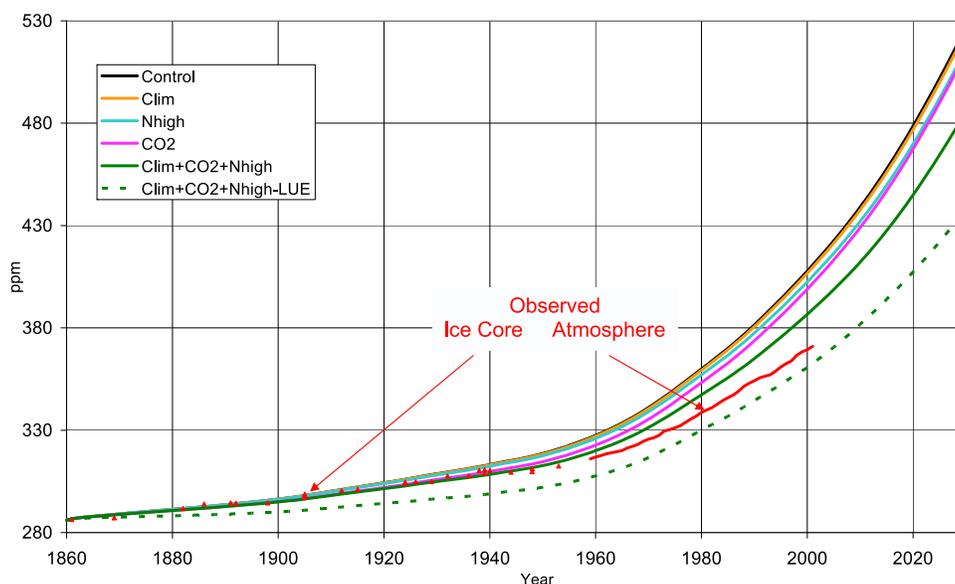


Figure 6. Response of atmospheric CO₂ concentration to increasing nitrogen deposition and changes in carbon uptake on land with present vegetation. “Clim + CO₂ + N_{high} -LU” scenario refers to model simulation excluding CO₂ emissions from land use change.

3.3. Uncertainties in Land and Ocean Responses

[34] In this study we were not able to quantify uncertainties associated with certain effects of nitrogen on land and ocean ecosystems. First, we did not include inhibiting effects of airborne pollutant nitrogen and high nitrogen loads on land ecosystems. These effects comprise increase in export of dissolved organic carbon and nitrogen rather than enhanced forest growth [Pregitzer *et al.*, 2004], forest dieback in areas with nitrogen saturated soils [Galloway *et al.*, 2004; Likens *et al.*, 1996], and reduced vegetation productivity due to high ozone concentrations in areas with high nitrous oxide emissions [Chameides *et al.*, 1994]. All three above mentioned effects would dampen the positive effect of increased nitrogen availability on plant growth. These effects were not included in the model, because the mechanisms behind them in different ecosystems types are not well understood. Second, our model does not include the mechanism for nitrogen uptake through the stomata of leaves. Several field studies [Johnson and Lindberg, 1992; McLaughlin *et al.*, 1996] suggest that forest canopies can intercept dry atmospheric nitrogen and assimilate retained reactive nitrogen from air. It is a matter of debate how significant the proportion of total incoming inorganic nitrogen intercepted by the canopy is. The reported proportion ranges from 16% to 90%. If all intercepted nitrogen is taken up by foliage then the nitrogen-induced carbon sink may be higher than estimated in our study. Third, we did not account for responses of regrowing forests in Europe and North America to rising CO₂ and nitrogen deposition. A recent modeling study [Churkina *et al.*, 2007] however suggests that regrowing forests have higher carbon uptake in response to elevated nitrogen deposition than mature forests. Including response of regrowing forests would increase land carbon uptake estimated in our study. Finally, we assumed no response of marine biota to the nitrogen deposition to the surface ocean. Although there is evidence that atmospheric nitrogen deposition and river nitrogen supply can increase marine productivity [Cotrim da Cunha *et al.*, 2007; Fanning, 1989] of the coastal ocean, other studies [Knap *et al.*, 1986] suggest that deposition of atmospheric nitrogen has a minimal effect on the productivity of the euphotic zone. A recent review [Duce *et al.*, 2008] suggests that the effect of atmospheric deposition of anthropogenic nitrogen on the open ocean is twofold. On one hand it may account for up to ~3% of new marine biological production or ~ 0.3 PgC per year. On the other hand, this input of nitrogen may account for up to ~1.6 Tg of N₂O emitted per year. It means that ~10% of the ocean's uptake of atmospheric CO₂ may result from atmospheric nitrogen fertilization, leading to a decrease in radiative forcing, up to about two thirds of this amount to be offset by the increase in N₂O emissions.

4. Conclusions

[35] Increasing nitrogen deposition and the physiological effect of elevated atmospheric CO₂ on plants have the potential to increase the land carbon sink, to offset the rise of CO₂ concentration in the atmosphere, and to reduce global warming. The magnitude of this offset depends on

response of land ecosystems and possibly also ocean biota to the synergistic effect of nitrogen deposition and atmospheric CO₂ as well as to changes in the patterns of nitrogen deposition in the future. The land response will be driven by distribution of different ecosystems in current and emerging industrial regions and their possibly not only positive responses to simultaneously increasing atmospheric CO₂ and nitrogen deposition. Although croplands currently dominate industrial regions, there is a trend toward reforestation in Europe and North America. Regrowing forests are more sensitive to the rising CO₂ and nitrogen deposition than mature forests. Therefore reforestation would amplify the synergistic response and thereby play a more important role in climate change mitigation ('buying time') than currently thought.

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References

- Ainsworth, E. A., and S. P. Long (2005), What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂, *New Phytol.*, *165*, 351–372, doi:10.1111/j.1469-8137.2004.01224.x.
- Brovkin, V., J. Bendtsen, M. Claussen, A. Ganopolski, C. Kubatzki, V. Petoukhov, and A. Andreev (2002), Carbon cycle, vegetation, and climate dynamics in the Holocene: Experiments with the CLIMBER-2 model, *Global Biogeochem. Cycles*, *16*(4), 1139, doi:10.1029/2001GB001662.
- Brovkin, V., S. Sitch, W. Von Bloh, M. Claussen, E. Bauer, and W. Cramer (2004), Role of land cover changes for atmospheric CO₂ increase and climate change during the last 150 years, *Global Change Biol.*, *10*, 1253–1266, doi:10.1111/j.1365-2486.2004.00812.x.
- Chameides, W. L., P. S. Kasibhatla, J. Yienger, and H. Levy II (1994), Growth of continental scale metro-agro-plexes, regional ozone pollution, and world food production, *Science*, *264*, 74–76, doi:10.1126/science.264.5155.74.
- Churkina, G., and S. W. Running (1998), Contrasting climatic controls on the estimated productivity of different biomes, *Ecosystems*, *1*, 206–215, doi:10.1007/s100219900016.
- Churkina, G., and S. W. Running (2000), Investigating the balance between timber harvest and productivity of the global coniferous forests under global change, *Clim. Change*, *47*, 167–191, doi:10.1023/A:1005620808273.
- Churkina, G., et al. (2003), Analyzing the ecosystem carbon dynamics of four European coniferous forest using a biogeochemistry model, *Ecosystems*, *6*, 168–184, doi:10.1007/s10021-002-0197-2.
- Churkina, G., K. Trusilova, M. Vetter, and F. J. Dentener (2007), Contributions of nitrogen deposition and forest re-growth to land carbon uptake, *Carbon Balance Manage.*, *2*, 5, doi:10.1186/1750-0680-2-5.
- Cienciala, E., S. W. Running, A. Lindroth, A. Grelle, and M. G. Ryan (1998), Analysis of carbon and water fluxes from the NOPEX boreal forest: Comparison of measurements with Forest-BGC simulations, *J. Hydrol.*, *212–213*, 62–78, doi:10.1016/S0022-1694(98)00202-9.
- Claussen, M., V. Brovkin, A. Ganopolski, C. Kubatzki, V. Petoukhov, and S. Rahmstorf (1999), A new model for climate system analysis: Outline of the model and application to palaeoclimate simulations, *Environ. Model. Assess.*, *4*, 209–216, doi:10.1023/A:1019016418068.
- Cotrim da Cunha, L., E. T. Buitenhuis, C. Le Quere, X. Giraud, and W. Ludwig (2007), Potential impact of changes in river nutrient supply on global ocean biogeochemistry, *Global Biogeochem. Cycles*, *21*, GB4007, doi:10.1029/2006GB002718.
- 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.
- D'Antonio, C., and M. C. Mack (2006), Nutrient limitation in a fire-derived, nitrogen rich Hawaiian grassland, *Biotropica*, *38*, 458–467, doi:10.1111/j.1744-7429.2006.00170.x.
- DeLucia, E. H., D. J. Moore, and R. J. Norby (2005), Contrasting responses of forest ecosystems to rising atmospheric CO₂: Implications for the

- global C cycle, *Global Biogeochem. Cycles*, *19*, GB3006, doi:10.1029/2004GB002346.
- Dentener, F. J., et al. (2006), Nitrogen and sulfur deposition on regional and global scales: A multimodel evaluation, *Global Biogeochem. Cycles*, *20*, GB4003, doi:10.1029/2005GB002672.
- Duce, R. A., et al. (2008), Impacts of atmospheric anthropogenic nitrogen on the open ocean, *Science*, *320*, 893–897, doi:10.1126/science.1150369.
- Elser, J. J., et al. (2007), Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems, *Ecol. Lett.*, *10*, 1135–1142, doi:10.1111/j.1461-0248.2007.01113.x.
- Etheridge, D. M., L. P. Steele, R. L. Langenfelds, R. J. Francey, J.-M. Barnola, and V. I. Morgan (1996), Natural and anthropogenic changes in atmospheric CO₂ over the last 100 years from air in Antarctic ice and firm, *J. Geophys. Res.*, *101*, 4115–4128, doi:10.1029/95JD03410.
- Ewert, F., et al. (2007), Crop models, CO₂, and climate change, *Science*, *315*, 459–460, doi:10.1126/science.315.5811.459c.
- Fanning, K. A. (1989), Influence of atmospheric pollution on nutrient limitation in the ocean, *Nature*, *339*, 460–463, doi:10.1038/339460a0.
- Finzi, A., R. Sinsabaugh, T. Long, and M. Osgood (2006a), Microbial community responses to atmospheric carbon dioxide enrichment in a warm-temperate forest, *Ecosystems*, *9*, 215–226, doi:10.1007/s10021-005-0078-6.
- Finzi, A. C., et al. (2006b), Progressive nitrogen limitation of ecosystem processes under elevated CO₂ in a warm-temperate forest, *Ecology*, *87*, 15–25, doi:10.1890/04-1748.
- Finzi, A. C., et al. (2007), Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO₂, *Proc. Natl. Acad. Sci. U. S. A.*, *104*, 14,014–14,019, doi:10.1073/pnas.0706518104.
- 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.
- Galloway, J. N., et al. (2004), Nitrogen cycles: Past, present, and future, *Biogeochemistry*, *70*, 153–226, doi:10.1007/s10533-004-0370-0.
- Ganopolski, A., V. Petoukhov, S. Rahmstorf, V. Brovkin, M. Claussen, A. Eliseev, and C. Kubatzki (2001), CLIMBER-2: A climate system model of intermediate complexity. Part II: Model sensitivity, *Clim. Dyn.*, *17*, 735–751, doi:10.1007/s003820000144.
- Gill, R. A., L. J. Anderson, H. W. Polley, H. B. Johnson, and R. B. Jackson (2006), Potential nitrogen constraints on soils carbon sequestration under low and elevated atmospheric CO₂, *Ecology*, *87*, 41–52, doi:10.1890/04-1696.
- Henry, H., N. Chiariello, P. Vitousek, H. Mooney, and C. Field (2006), Interactive effects of fire, elevated carbon dioxide, nitrogen deposition, and precipitation on a California annual grassland, *Ecosystems*, *9*, 1066–1075, doi:10.1007/s10021-005-0077-7.
- Holland, E. A., et al. (1997), Variation in the predicted spatial distribution of atmospheric nitrogen deposition and their impact on carbon uptake by terrestrial ecosystems, *J. Geophys. Res.*, *102*, 15,849–15,866, doi:10.1029/96JD03164.
- 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.
- Hungate, B. A., et al. (2006), Nitrogen cycling during seven years of atmospheric CO₂ enrichment in a scrub oak woodland, *Ecology*, *87*, 26–40, doi:10.1890/04-1732.
- Janssens, I. A., et al. (2003), Europe's terrestrial biosphere absorbs 7 to 12% of European anthropogenic CO₂ emissions, *Science*, *300*, 1538–1542, doi:10.1126/science.1083592.
- Johnson, D. W., and S. E. Lindberg (1992), *Atmospheric Deposition and Forest Nutrient Cycling*, 707 pp., Springer, New York.
- Jones, C. J., P. M. Cox, R. L. H. Essery, D. L. Roberts, and M. J. Woodage (2003), Strong carbon cycle feedbacks in a climate model with interactive CO₂ and sulphate aerosols, *Geophys. Res. Lett.*, *30*(9), 1479, doi:10.1029/2003GL016867.
- Jung, M., M. Herold, K. Henkel, and G. Churkina (2006), Exploiting synergies of land cover products for carbon cycle modelling, *Remote Sens. Environ.*, *101*, 534–553, doi:10.1016/j.rse.2006.01.020.
- Kalnay, E., et al. (1996), The NCEP/NCAR reanalysis project, *Bull. Am. Meteorol. Soc.*, *77*, 437–471, doi:10.1175/1520-0477(1996)077<0437:TNYRP>2.0.CO;2.
- King, A. W., et al. (Eds.) (2007), *The First State of the Carbon Cycle Report (SOCCR): The North American Carbon Budget and Implications for the Global Carbon Cycle*, 242 pp., U.S. Clim. Change Sci. Program, Washington, D. C.
- King, J. S., P. J. Hanson, E. Bernhardt, P. DeAngelis, R. J. Norby, and K. S. Pregitzer (2004), A multiyear synthesis of soil respiration responses to elevated atmospheric CO₂ from four forest FACE experiments, *Global Change Biol.*, *10*, 1027–1042, doi:10.1111/j.1529-8817.2003.00789.x.
- Knap, A. H., T. D. Jickells, A. Pszenny, and J. N. Galloway (1986), The significance of atmospheric derived fixed nitrogen on the productivity of the Sargasso Sea, *Nature*, *320*, 158–160, doi:10.1038/320158a0.
- Kulkarni, M. V., P. M. Groffman, and J. B. Yavitt (2008), Solving the global nitrogen problem: It is a gas!, *Front. Ecol. Environ.*, *6*, 199–206, doi:10.1890/060163.
- LeBauer, D. S., and K. K. Treseder (2008), Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed, *Ecology*, *89*, 371–379, doi:10.1890/06-2057.1.
- Likens, G. E., C. T. Driscoll, and D. C. Buso (1996), Long-term effects of acid rain: Response and recovery of a forest ecosystem, *Science*, *272*, 244–246, doi:10.1126/science.272.5259.244.
- Lloyd, J. (1999), The CO₂ dependence of photosynthesis, plant growth responses to elevated CO₂ concentrations and their interaction with soil nutrient status: II. Temperate and boreal forest productivity and the combined effects of increasing CO₂ concentrations and increased nitrogen deposition at a global scale, *Funct. Ecol.*, *13*, 439–459, doi:10.1046/j.1365-2435.1999.00350.x.
- Magnani, F., et al. (2007), The human footprint in the carbon cycle of temperate and boreal forests, *Nature*, *447*, 849–851.
- McLaughlin, J. W., I. J. Fernandez, and K. J. Richards (1996), Atmospheric deposition to a low-elevation spruce-fir forest, Maine, USA, *J. Environ. Qual.*, *25*, 248–259.
- Nadelhoffer, K. L., et al. (1999), Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests, *Nature*, *398*, 145–148, doi:10.1038/18205.
- Norby, R. J., and C. M. Iversen (2006), Nitrogen uptake, distribution, turnover, and efficiency of use in a CO₂ enriched sweetgum forest, *Ecology*, *87*, 5–14, doi:10.1890/04-1950.
- Oren, R., et al. (2001), Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere, *Nature*, *411*, 469–472, doi:10.1038/35078064.
- Pepper, D. A., S. J. Del Grosso, R. E. McMurtrie, and W. J. Parton (2005), Simulated carbon sink response of shortgrass steppe, tallgrass prairie and forest ecosystems to rising [CO₂], temperature and nitrogen input, *Global Biogeochem. Cycles*, *19*, GB1004, doi:10.1029/2004GB002226.
- Petoukhov, V., A. Ganopolski, V. Brovkin, M. Claussen, A. Eliseev, C. Kubatzki, and S. Rahmstorf (2000), CLIMBER-2: A climate system model of intermediate complexity. Part I: Model description and performance for present climate, *Clim. Dyn.*, *16*, 1–17, doi:10.1007/PL00007919.
- Pregitzer, K. S., D. R. Zak, A. J. Burton, J. A. Ashby, and N. W. Macdonald (2004), Chronic nitrate additions dramatically increase the export of carbon and nitrogen from northern hardwood ecosystems, *Biogeochemistry*, *68*, 179–197, doi:10.1023/B:BIOG.0000025737.29546.f0.
- Raupach, M. R., G. Marland, P. Ciais, C. Le Que, J. G. Canadell, G. Klepper, and C. B. Field (2007), Global and regional drivers of accelerating CO₂ emissions, *Proc. Natl. Acad. Sci. U. S. A.*, *104*, 10,288–10,293, doi:10.1073/pnas.0700609104.
- Reich, P. B., et al. (2006), Nitrogen limitation constrains sustainability of ecosystem response to CO₂, *Nature*, *440*, 922–925, doi:10.1038/nature04486.
- Rodhe, H., F. J. Dentener, and M. Schulz (2002), The global distribution of acidifying wet deposition, *Environ. Sci. Technol.*, *36*, 4382–4388, doi:10.1021/es020057g.
- Running, S. W., and E. R. J. Hunt (1993), Generalization of a forest ecosystem process model for other biomes, Biome-BGC, and an application for global-scale models, in *Scaling Physiological Processes: Leaf to Globe*, edited by J. R. Ehleringer and C. B. Field, pp. 141–158, Academic, San Diego, Calif.
- Solomon, S., et al. (Eds.) (2007), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, 996 pp., Cambridge Univ. Press, U. K.
- Tanner, E. V. J., P. Vitousek, and E. Cuevas (1998), Experimental investigation of nutrient limitation of forest growth on wet tropical mountains, *Ecology*, *79*, 10–22.
- Thornton, P. E. (Ed.) (1998), *Regional Ecosystem Simulation: Combining Surface- and Satellite-Based Observations to Study Linkages between Terrestrial Energy and Mass Budgets*, 280 pp., Univ. of Montana, Missoula.
- Thornton, P. E., et al. (2002), Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests, *Agric. For. Meteorol.*, *113*, 185–222, doi:10.1016/S0168-1923(02)00108-9.

- Thornton, P. E., J.-F. Lamarque, N. A. Rosenbloom, and N. M. Mahowald (2007), Fundamental influence of terrestrial carbon-nitrogen cycle coupling on modeled CO₂ fertilization and climate-carbon cycle dynamics, *Global Biogeochem. Cycles*, *21*, GB4018, doi:10.1029/2006GB002868.
- Townsend, A. R., B. H. Braswell, E. A. Holland, and J. E. Penner (1996), Spatial and temporal patterns in terrestrial carbon storage due to deposition of fossil fuel nitrogen, *Ecol. Appl.*, *6*, 806–814, doi:10.2307/2269486.
- Trusilova, K., J. Trembath, and G. Churkina (2009), Parameter estimation and validation of the terrestrial ecosystem model BIOME-BGC using eddy-covariance flux measurements, *Tech. Rep. 16*, 62 pp., Max-Planck Inst. for Biogeochem., Jena.
- Vetter, M., C. Wirth, H. Böttcher, G. Churkina, E. D. Schulze, T. Wutzler, and G. Weber (2005), Partitioning direct and indirect human-induced effects on carbon sequestration of managed coniferous forests using model simulations and forest inventories, *Global Change Biol.*, *11*, 810–827, doi:10.1111/j.1365-2486.2005.00932.x.
- Vitousek, P., L. O. Edin, P. A. Matson, J. H. Fownes, and J. Neff (1998), Within-system element cycles, input-output budgets, and nutrient limitations, in *Success, Limitations, and Frontiers in Ecosystem Science*, edited by M. Pace and P. Groffman, pp. 432–451, Springer, New York.
- Vitousek, P., S. Hättenschwiler, L. Olander, and S. Allison (2002), Nitrogen and nature, *Ambio*, *2*, 97–101.
- White, M. A., P. E. Thornton, S. W. Running, and R. R. Nemani (2000), Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: Net primary production controls, *Earth Interact.*, *4*, 1–85, doi:10.1175/1087-3562(2000)004<0003:PASAOT>2.0.CO;2.
- Xia, J., and S. Wan (2008), Global response patterns of terrestrial plant species to nitrogen addition, *New Phytol.*, *179*, 428–439, doi:10.1111/j.1469-8137.2008.02488.x.
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- V. Brovkin and W. von Bloh, Potsdam Institute for Climate Impact Research, PO Box 60 12 03, D-14412 Potsdam, Germany.
- G. Churkina, M. Jung, and K. Trusilova, Max Planck Institute for Biogeochemistry, Hans-Knöll-Str. 10, D-07745 Jena, Germany.
- F. Dentener, Joint Research Centre, Institute for Environment and Sustainability, European Commission, Via E. Fermi 2749, I-21027, Ispra, Italy.