Open access • Journal Article • DOI:10.1111/J.1365-2486.2010.02261.X

Feedback of carbon and nitrogen cycles enhances carbon sequestration in the terrestrial biosphere — Source link

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Published on: 01 Feb 2011 - Global Change Biology (Blackwell Science)

Topics: Nitrogen cycle, Reactive nitrogen, Human impact on the nitrogen cycle, Carbon sequestration and Denitrification

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To cite this version:

Gerd A. Esser, Jens Kattge, Abdulla Sakalli. Feedback of carbon and nitrogen cycles enhances carbon sequestration in the terrestrial biosphere. Global Change Biology, Wiley, 2010, 17 (2), pp.819. 10.1111/j.1365-2486.2010.02261.x . hal-00599519

Global Change Biology

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Journal:	*Global Change Biology*
Manuscript ID:	GCB-10-0229
Wiley - Manuscript type:	Primary Research Articles
Date Submitted by the Author:	12-Mar-2010
Complete List of Authors:	Esser, Gerd; Justus-Liebig-University, Institute for Plant Ecology Kattge, Jens; Max-Planck-Institute for Biogeochemistry Sakalli, Abdulla; Justus-Liebig-University, Institute for Plant Ecology
Keywords:	carbon cycle, nitrogen cycle, carbon sequestration, carbon dioxide, carbon nitrogen model
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Feedback of carbon and nitrogen cycles enhances carbon sequestration in the terrestrial biosphere

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March 2010

Abstract

The efforts to explain the "missing sink" for anthropogenic carbon dioxide have included in recent years the role of nitrogen as an important constraint for biospheric carbon fluxes. We used the Nitrogen Carbon Interaction Model (NCIM) to investigate patterns of carbon and nitrogen storage in different compartments of the terrestrial biosphere as a consequence of a rising atmospheric CO_2 concentration, in combination with varying levels of nitrogen availability. This model has separate but closely coupled carbon and nitrogen cycles with a focus on soil processes and soil–plant interactions, including an active compartment of soil microorganisms decomposing litter residues and competing with plants for available nitrogen. Biological nitrogen fixation is represented as a function of vegetation nitrogen demand. The model was validated against several global datasets of soil and vegetation carbon and nitrogen pools. Five model experiments were carried out for the modeling periods 1860–2002 and 2002–2100. In these experiments we varied the nitrogen availability using different combinations of biological nitrogen fixation, denitrification, leaching of soluble nitrogen compounds with constant or rising atmospheric CO_2 concentrations. Oversupply with nitrogen, in an experiment with nitrogen fixation, but no nitrogen losses, together

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with constant atmospheric CO_2, led to some carbon sequestration in organismic pools, which was nearly compensated by losses of C from soil organic carbon pools. Rising atmospheric CO_2 always led to carbon sequestration in the biosphere. Considering an open nitrogen cycle including dynamic nitrogen fixation, and nitrogen losses from denitrification and leaching, the carbon sequestration in the biosphere is of a magnitude comparable to current observation based estimates of the “missing sink”. A fertilization feedback between the carbon and nitrogen cycles occured in this experiment which was much stronger than the sum of separate influences of high nitrogen supply and rising atmospheric CO_2. The demand–driven biological nitrogen fixation was mainly responsible for this result. For the modeling period 2002–2100, NCIM predicts continued carbon sequestration in the low range of previously published estimates, combined with a plausible rate of CO_2 driven biological nitrogen fixation and substantial redistribution of nitrogen from soil to plant pools.

1 Introduction

The terrestrial biosphere is a major player in the global carbon cycle (Meehl *et al.* 2007). The terrestrial living phytomass (mass of all land plants) contains about 550 ± 100 Pg[1] of carbon (Houghton 2007), the dead phytomass (litter) about 100 Pg C, the soil organic carbon about 1 500–2 000 Pg C (Jobbágy & Jackson 2000). The preindustrial atmosphere contained 600 Pg of carbon as carbon dioxide (CO_2).

Since preindustrial times, 343 Pg of carbon have been emitted from fossil sources by human activities (Marland *et al.* 2007). Another 156 Pg of carbon were released to the atmosphere from global changes in land use (Houghton 2007). The total anthropogenic carbon emission to the atmosphere thus amounts to 499 Pg since preindustrial times. 216 Pg C was stored in the atmosphere (airborne fraction), which lead to an increase of the CO_2 concentration from 280 ppm to 385 ppm in 2008 (estimated after Keeling (2005)). The uptake into the oceanic buffer system was about 118 ± 19 Pg C (Sabine *et al.* 2004). The difference between these sources and sinks is 165 Pg C. It is commonly assumed that this carbon is stored somewhere in the terrestrial biosphere, and referred to as “missing sink”.

The processes which might enable the terrestrial biosphere to sequester such an amount of carbon, and their interactions and limitations, are not yet completely

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[1] 1 Pg = 1 Gt = 10^{15}g

understood. Photosynthesis by green plants produces only carbohydrates. Nitrogen and other elements are necessary to bind (allocate) this assimilated carbon in the phytomass. Here nitrogen is especially relevant as it is required for nucleic acids, proteins, chlorophyll and other porphyrinoids, alkaloids and other secondary plant substances. Nitrogen is also present in humic substances and soil microorganisms and thus in soil organic matter.

There is further evidence that parameters of the photosynthetic carbon turnover, i.e. the carboxylation capacity, the maximum photosynthesis rate, and others (Kattge *et al.* 2009; Wright *et al.* 2004), as well as the autotrophic respiration (Kattge 2002; Reich *et al.* 2006c; Reich *et al.* 2008) are influenced by the plant tissue nitrogen content.

It is therefore a prerequisite for the prediction of the global carbon balance for the next century to understand and quantify the interactions of the global carbon and nitrogen cycles (Hungate *et al.* 2003). However, information on the interaction of these systems and on the regulation of the relevant biospheric processes under global change conditions is still scarce (Wang *et al.* 2007).

The carbon to nitrogen (C/N) ratios in the different biospheric compartments are widely varying (Clüsener Godt 1989): Herbaceous phytomass has a mean[2] C/N ratio of about 31 ± 7, woody phytomass about 169 ± 43. In soil organic matter, the residues of decomposed lignins from litter are free of nitrogen. Humic substances which are products of biological soil processes have variable C/N ratios of about 15–20. Soil organisms have C/N ratios from 5 (bacteria dominant) to 12 (fungi dominant). The quality of litter in terms of nitrogen and lignin content tends to affect the type of soil organisms to dominate (Corbeels *et al.* 2005; Henriksen & Breland 1999). Soil microorganisms decompose plant litter and soil organic matter. These materials provide very wide C/N ratios relative to the own requirements of soil organisms (Vitousek *et al.* 2002). They therefore compete with plants for the mobile (available and adsorbed) nitrogen in soil.

The major fluxes in the terrestrial carbon cycle include the atmospheric CO_2 pool. The net carbon input flux from the atmosphere into the green plants and thus into the biosphere amounts to about 60 $\mathrm{Pg{\cdot}yr^{-1}}$ (Houghton 2007).

The major fluxes in the terrestrial nitrogen cycle occur between vegetation, litter, and soil. The annual nitrogen turnover in this major portion of the nitrogen cycle amonts to about 1.1–1.5 $\mathrm{Pg{\cdot}yr^{-1}}$.

In contrast, relatively small fluxes connect the huge atmospheric nitrogen pool with the biosphere (Galloway & Cowling 2002). Following Rosswall (1976) we

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[2] Means of available analyses of plant material, not area–weighted global means.

therefore call all fluxes which connect the biosphere with the atmospere and the hydrosphere “minor” fluxes, in this paper. Nitrogen fixing organisms, which live free in soil or water bodies and other habitats, or are symbionts in roots of legumes and several other groups of plants, produce reactive nitrogen from atmospheric N_2. This biological nitrogen fixation amounts to about 130 $\mathrm{Tg \cdot yr^{-1}}$ (Galloway *et al.* 2004). A small input of reactive nitrogen into the biosphere in the order of magnitude of 2–5% of the biological nitrogen fixation comes from the oxidation of N_2 by lightnings (Lelieveld & Dentener 2000). There is also input of reactive nitrogen into the terrestrial biosphere from anthropogenic emissions of about 25 $\mathrm{Tg \cdot yr^{-1}}$ (Galloway *et al.* 2004). Other minor fluxes cause nitrogen losses from the biosphere. Those include leaching of soluble nitrogen compounds to groundwater and to water outfalls (Boyer *et al.* 2006), and denitrification, i.e. the transfer of reactive nitrogen to non reactive N_2 or other gaseous compounds like N_2O (Barnard *et al.* 2005; Hirsch *et al.* 2006).

The total amount of nitrogen in the terrestrial biosphere may only change as a consequence of imbalanced minor fluxes. But the change of the nitrogen content of individual biospheric pools may also occur by redistribution from other biospheric pools. Both, the minor exchange fluxes and the redistribution fluxes are important for the potential of the biosphere to store carbon. Nitrogen limited biospheric pools or processes are most susceptible to changes in the nitrogen balance. As a consequence of the rising atmospheric CO_2 concentration also systems which are currently not considered to be nitrogen limited may become limited by the nitrogen availability due to the improved availability of assimilates in plants which may lead to wider C/N ratios in phytomass and litter (McMurtrie *et al.* 2001; Oren *et al.* 2001; Pepper *et al.* 2005, 2007; Reich *et al.* 2006b). Reduced decomposition rates of litter may result. With rising atmospheric CO_2, the ability of these systems to store additional carbon may then be controlled, or at least be influenced, by those nitrogen exchanges and redistribution fluxes.

We used the Nitrogen Carbon Interaction Model (NCIM) (Esser 2007) to investigate the carbon and nitrogen storage in the terrestrial biosphere, as influenced by the rising atmospheric CO_2 concentration together with different combinations of the minor nitrogen exchange fluxes, at the global scale. We concentrated on two different periods: A historical study for the period 1860–2002, and future projections from 2002–2100.

2 Materials and Methods

2.1 NCIM Model description

NCIM is a global generic model with separate and closed, but intensively coupled carbon (C) and nitrogen (N) cycles. It accounts for C and N processes and the feedbacks in plants and soil known to be relevant. NCIM emphasizes soil processes, soil–plant nitrogen interaction, and the competition for nitrogen between soil organisms and plants. A detailed documentation of the model, which includes the structures of the model and of the program code and all equations, is found at Esser (2007).

The model is regionalized on a 0.5 degrees grid of geographical latitude and longitude. The time resolution for slow processes is one month, for fast processes one day. The model uses a global digital vegetation data set on the 0.5 degrees grid, derived from the Atlas for Biogeography (Schmithüsen 1976), which includes 176 vegetation units. These units were aggregated to 31 biomes, for which vegetation dependent parameters were quantified (table 3). The model uses a digitalization of the soil map of the world (FAO–Unesco 1974 ff.) which provides the dominant soil unit for each grid element. Long term means for monthly temperature and monthly precipitation for each grid element were implemented from Leemans & Cramer (1991).

The mass balance equations are solved using an explicitly programmed 4th–order Runge–Kutta method, which subdivides the basic model time step of one day further into integration steps, thus ensuring model stability and helping prevent integration biases.

NCIM has closed carbon and nitrogen cycles. Mass conservation in both cycles is maintained (see figure 1). Carbon and nitrogen transport between the respective pools occurs by processes (fluxes). The carbon pools in each grid element of the model include: Four compartments in living phytomass (leaf, wood, coarse root and fine root), four compartments in litter, respectively, lignin compounds, humic substances, and carbon in the biomass of soil microorganisms. The nitrogen pools are: four compartments in living phytomass, four compartments in litter, reserve nitrogen stored in plants, available (soluble) nitrogen in litter and soil, nitrogen in the biomass of soil microorganisms, humic substances, and nitrogen adsorbed to clay and polyphenols of humic substances (soil N buffer, immobilized ammonium (Vitousek *et al.* 2002)).

Amounts of carbon or nitrogen and C/N ratios are not prescribed during a model run. Rather, the actual C/N ratios of all relevant phytomass and soil compartments are recalculated in each model time step, by division of the respective pools. Information on the system state (i.e. the actual values of pools or state variables) is used in each time step to steer or regulate processes (fluxes), which transport nitrogen or carbon from one pool to another. Influences of nitrogen pools on carbon fluxes and *vice versa* couple the nitrogen and carbon cycles (bold black arrows in figure 1).

Model parameters were optimized in an inverse approach against data from soil profile analyses (FAO–Unesco 1974 ff.) and ecosystem databases (Esser *et al.* 2000).

In the following, we explain the methods used to describe the major nitrogen and carbon processes of the bispheric N and C cycles, in particular the uptake of available nitrogen by plants and soil organisms, and the small but very important fluxes of nitrogen into and out of the terrestrial biosphere which we call minor fluxes: The fixation of atmospheric nitrogen by microorganisms, the processes of denitrification from soil, and the leaching of soluble nitrogen from the soil into the groundwater and the outfalls.

The array denominators i, im, is, ib are used in the following equations. Their meaning and their dimensions are explained in table 1.

The central pool to provide nitrogen to plants and soil organisms is the soluble, available nitrogen pool (avn) in the soil and litter. Plants and soil organisms compete for the nitrogen from this pool. This competition is the result of the seasonally different affinity for avn of the uptake fluxes by plant roots and soil organisms:

The uptake of soluble nitrogen from soil by plant roots ($avunf$) depends on the actual leaf carbon $pcha$, and the nitrogen in the target pool $resn$ (mobile reserve nitrogen in plants) and in the source pool avn.

$$\begin{aligned} avunf(i) &= cassn(i) \cdot pcha(i) \\ &\quad \cdot \frac{2}{1. + exp(resn(i) - resn0(i))} \\ &\quad \cdot avn(i)^{zavn} \end{aligned} \tag{1}$$

$resn0$ is a long–term (200 years) running mean of $resn$. The term in line 2 regulates the uptake according to the actual nitrogen state of the plants, but allows also the long–term adaptation of the vegetation to changes of the nitrogen status. The exponent $zavn < 1$ in line 3 uncouples the uptake from the direct linear influence of avn, and simulates active uptake of N by plant roots. The coefficient of uptake $cassn$ has a maximum value of 0.013 [gN/gC/month] and is modified by the deviation of the mean temperature of the actual month it from the mean temperature of the warmest month $mtwam$ using a Q_{10} of two:

$$\begin{aligned} q_{10} &= 2.0 \\ x &= \frac{\ln q_{10}}{10} \\ cassn(i) &= 0.013 \cdot \mathrm{e}^{x \cdot (it(i,im) - mtwam(i))} \end{aligned} \tag{2}$$

The available humidity is important for the uptake of nitrogen by plants but it is already implicitly considered by the variable $pcha$ in equation (1), since the leaf phytomass depends on the actual humidity regime in water–limited biomes.

The allocation of nitrogen from the reserve pool $resn$ to plant biomass depends on the amount of allocated carbon, the size of the nitrogen reserve pool, and is corrected by the actual nitrogen state of the plant tissues. For the allocation to aboveground herbaceous phytomass nitrogen it reads:

$$\begin{aligned} nppnha(i) &= calha(i) \\ & \quad \cdot \left(\frac{resn(i)}{resn0(i)} \right)^{zalloc} \\ & \quad \cdot 10^{\min\left(1, \frac{\ln \frac{cnacha(i)}{cnh(ib(i))}}{(\ln 2.)^3}\right)} \end{aligned} \tag{3}$$

$$\begin{aligned} \text{with :} & \\ calha(i) &= \frac{nppha(i)}{cnh(ib(i))} \end{aligned} \tag{4}$$

Similar equations are used for the allocation to the other three phytomass compartments $nppnhb$, $nppnwa$, and $nppnwb$.

The allocation of carbon $nppha$ through $nppwb$ (equations (7) – (10)) to the four different phytomass compartments depends on the actual nitrogen status of the leaves, which is calculated from the actual state of the respective pools:

$$cnacha(i) = \frac{pcha(i)}{pnha(i)} \tag{5}$$

Nitrogen–independent monthly allocation fluxes $npphao$ through $nppwbo$ are calculated for the four phytomass campartments from the monthly climatic variables and further modified by a correction function derived from the actual atmospheric CO_2 concentration (Esser 1991; Esser *et al.* 1994). Sampled correction factors from this function are 0 for 80 ppm, 0.92 for 280 ppm, 1.00 for 320 ppm, and 1.21 for 600 ppm.

In the next step, these nitrogen–independent allocation fluxes are corrected according to the 30–days running means of the deviation of the actual C/N ratio in the leaves from a biome–typical standard C/N ratio $cnh(i)$ (table 3). The variable $fnmeano$ in equation (6) refers to the value of $fnmean$ of the day before.

$$\begin{aligned}
x &= \frac{cnh(ib(i))}{cnacha(i)} \\
fn &= 1.7465 \cdot (1 - \mathrm{e}^{-1.7\cdot(x-0.5)}) \\
fnmean(i) &= \frac{fnmeano(i)\cdot(30-1)+fn}{30} && (6) \\
nppha(i) &= fnmean(i)\cdot npphao(i) && (7) \\
npphb(i) &= fnmean(i)\cdot npphbo(i) && (8) \\
nppwa(i) &= fnmean(i)\cdot nppwao(i) && (9) \\
nppwb(i) &= fnmean(i)\cdot nppwbo(i) && (10)
\end{aligned}$$

Litter production in NCIM is calculated on a monthly basis. Months with litter fall are not prescribed. They are determined on the basis of the monthly climate at the beginning of each model year. A vegetation specific part $rcych$ of leaf litter N is recycled to the plant reserve N before leaves are shed (for $rcych$ see table 3). Litter as well as humic substances and lignin residuals, are consumed by microorganisms.

The uptake of available nitrogen by soil organisms $avunf$ depends on the soluble nitrogen pool avn and on the suitability of the climatic conditions of a given month for organismic activity, $cgmic$.

$$mignf(i) = cgmic(i)\cdot avn(i)^{zmign} \tag{11}$$

The exponent $zmign < 1$ decouples the uptake flux from the linear influence of the source pool avn and simulates active N uptake. The coefficient $cgmic$ is a complex function of the mean monthly temperature (it) and the monthly precipitation (ipp).

$$cgmic(i) = 15\cdot cldh(i) \tag{12}$$

$$\begin{aligned}
cldh(i) &= \exp\left(p_1 + p_2\cdot\ln(ipp(i,im)) - p_3\cdot ipp(i,im)^{p_4}\right) \\
&\quad + \exp(p_5)\cdot\tanh(p_6\cdot ipp(i,im)) && (13)
\end{aligned}$$

with the parameters

$$
\begin{aligned}
p_1 &= -1.96628 \cdot (it(i,im) - 5) - 12.39641 \\
p_2 &= 0.002236189 \cdot (it(i,im) + 55)^2 \\
p_3 &= 4.568434 \cdot \exp(-0.1041649 \cdot (it(i,im) - 5)) \\
p_4 &= 0.0001132567 \cdot (it(i,im) + 55)^2 \\
p_5 &= 0.07315304 \cdot (it(i,im) - 5) - 3.51145 \\
p_6 &= \exp\Big(\frac{15000}{(it(i,im) + 55)^2} - 6.5\Big)
\end{aligned}
$$

and the restrictions

$$
\begin{array}{lllll}
\text{If} & ipp(i,im) & = & 0.0 & \text{then} \quad cldh(i) = 0.0 \\
\text{If} & it(i,im) & < & -30.0 & \text{then} \quad cldh(i) = \exp(p_5) \cdot \tanh(p_6 \cdot ipp(i,im))
\end{array}
$$

For a list of data used to develop function (13) see Esser (1986). A plot of equation (13) is found in figure 2.

The flux $mignf$, equation (11), provides nitrogen for the microorganismic growth. The respective carbon is provided from the uptake of litter, soil humus, and lignin residuals. These compounds have a wider C/N ratio than soil organisms or, in the case of lignin, contain no nitrogen at all. $mignf$ thus influences the uptake and depletion of those compounds by soil organisms. Soil organisms dominate the avn utilization if fresh litter with a wide C/N ratio is present. The plants are most competitive during their growing season when leaves ($pcha$) promote the uptake of avn. This behavior of NCIM is supported by observations in natural and agricultural ecosystems (see Hungate at al. 1999). Since soil organisms are short–lived, their mortality recycles N.

In NCIM, the carbon of litter, lignin, and humic substances is consumed by soil organisms and incorporated into their carbon pool. On the other side, soil organisms lose carbon through the processes respiration, mortality, and output of excess carbon if they feed on carbon-rich components. All three processes are assumed to be proportional to the carbon pool of the soil organisms ($micc$) and are the only processes which mineralize organic material to CO_2 in NCIM:
Respiration of microorganisms:

$$mircf(i) = crmic(i) \cdot micc(i) \tag{14}$$

The respiration coefficient $crmic$ is the basic metabolic turnover of the soil organisms. It depends on temperature according to $Q_{10} = 2$ with a base–temperature of

20°C:

$$\begin{aligned} q_{10} &= 2.0 \\ x &= \frac{\ln q_{10}}{10} \\ crmic(i) &= 0.05 \cdot \mathrm{e}^{x\cdot(it(i,im)-20)} \end{aligned} \tag{15}$$

Mortality of soil organisms:

$$mimcf(i) = cmmic(i) \cdot micc(i) \tag{16}$$

It is assumed that the life span of soil organisms depends on their activity $cldha$, see equation (13):

$$cmmic(i) = 0.1 \cdot cldha(i) \tag{17}$$

Output of excess CO_2 by microorganisms if they feed on carbon–rich compounds (Manzoni *et al.* 2008). The variable $cnmic$ is the actual C/N ratio of the biomass of soil organisms. The saturation function has half–saturation at $cnmic = 9$. The coefficient is scaled to $3/4$ per month or 0.025 per day.

$$\begin{aligned} miscf(i) &= \frac{max(6, cnmic(i)) - 6}{max(6, cnmic(i)) - 3} \\ &\quad \cdot \frac{3}{4} \cdot micc(i) \end{aligned} \tag{18}$$

There is a loss of avn from soil by leaching into ground water and outfalls.

$$leanf(i) = cleach(i) \cdot avn(i) \tag{19}$$

The coefficient $cleach$ depends on the water saturation of the soil and the composition (sand fraction) of the soil material. It is zero if the precipitation of the month is zero or less than the actual evapotranspiration $aetm$ or if the temperature is less than zero (frozen water):

$$\begin{aligned} cleach(i) &= 0 \begin{cases} \text{for} & ipp(i,im) = 0 \\ \text{or} & ipp(i,im) < aetm(i,im) \\ \text{or} & it(i,im) < 0 \end{cases} \\ & \quad \text{else:} \\ cleach(i) &= (0.1 + sand(i)) \cdot \left(1 - \min\left(1, \frac{aetm(i,im)}{ipp(i,im)}\right)\right) \end{aligned} \tag{20}$$

The factor 0.1 in equation (20) takes into account that leaching may occur even if there is no sand in the soil. $sand = 0, \ldots, 1$ is the sand–fraction of the dominating soil type in a given grid element, and was obtained from the Global Ecosystems Database: Near Surface Soil Texture File (Staub & Rosenzweig 1987) and regridded to NCIM's 0.5 degree grid. The conversion of the texture classes of this file into the sand fraction is found in table 2. For the calculation of the monthly actual evapotranspiration we use an algorithm suggested by Prentice *et al.* (1992).

In NCIM, available nitrogen is adsorbed to the clay and humus components of the soil (Vitousek *et al.* 2002). This keeps the concentration of mobile nitrogen (avn) low and minimizes losses by leaching. However, it has only minor influence on the uptake of avn by plants and soil organisms due to the exponents $zavn$ and $zmign$ used in equations (1) and (11). The capacity to bind soluble nitrogen compounds depends on the fraction of fine material (clay) in the soil, and on the amount of humic substances. Therefore it may vary with time and season. The adsorption flux $avnpuf$ is a function of the available nitrogen pool. The desorption $puavnf$ depends on the adsorbed nitrogen pool and increases with decreasing free binding capacity, i.e. increasing load of adsorbed N:

$$avnpuf(i) = cavnpu(i) \cdot avn(i) \tag{21}$$

$$cavnpu(i) = 10 \tag{22}$$

The actual adsorption–capacity cap of the soil is calculated as:

$$\begin{aligned} cap(i) = {} & (1 - sand(i)) \cdot fsoil(is(i)) \cdot 105 \qquad \text{(from clay minerals)} \\ & + humc(i) \cdot 3.5 \cdot 10^{-2} \qquad \text{(from humic compounds)} \end{aligned} \tag{23}$$

The factor $fsoil$ in equation (23) refers to a soil–fertility factor for the dominating soil unit of a given grid element (description and values see Esser 1991) and considers the declining exchange capacity of the different clay minerals (montmorillonitic, kaolinitic, gibbsitic clay minerals). The values 105 and $3.5 \cdot 10^{-2}$ for the specific adsorption capacities of clay and humus are means of soil analyses by FAO–Unesco (1974 ff.). $puffn$ is the actual pool of adsorbed nitrogen.

$$\begin{aligned} cpuavn(i) &= \frac{cavnpu(igrid)}{60} \\ puavnf(i) &= cpuavn(i) \\ & \quad \cdot \frac{cap(i)}{cap(i) - puffn(i)} \\ & \quad \cdot puffn(i) \end{aligned} \tag{24}$$

Another loss of nitrogen from the terrestrial biosphere is the denitrification flux, $n2onf$, from available nitrogen to N_2O and N_2. We adopted an algorithm proposed by Nevison *et al.* (1996) which assumes that denitrification depends on net mineralization $mimnf$.

$$n2onf(i) = \begin{cases} 9.5 \cdot 10^{-4} \cdot mimnf(i) & \text{for} \quad mimnf \leq 2.3 \\ \left.\begin{array}{l} 7.2 \cdot 10^{-5} \cdot mimnf(i)^2 \\ \quad + 3.3 \cdot 10^{-4} \cdot mimnf(i) \\ \quad + 1.0 \cdot 10^{-3} \end{array}\right\} & \text{for} \quad mimnf > 2.3 \end{cases} \tag{25}$$

Equations (26) through (28) provide descriptions of the fixation of atmospheric N_2 by symbiontic microorganisms (see Gibson *et al.* 1983). The fixation rate depends on the distribution and density of the host plants in each of the 176 vegetation units, respectively in the 31 biomes, their actual productivity, and their amount of reserve nitrogen, i.e. their nitrogen demand. In NCIM, the rising atmospheric CO_2 concentration enhances N_2 fixation because it increases the C and N allocation in plants, thus reducing their reserve nitrogen pool and increasing the N demand.
Nitrogen fixation by symbionts in legume roots:

$$\begin{aligned} legnf(i) &= legnpp(ib(i)) \cdot 0.3 \\ &\quad \cdot \frac{resn0(i)}{resn(i)} \\ &\quad \cdot \left(\frac{nppha(i) + npphb(i)}{cnh(ib(i))} + \frac{nppwa(i) + nppwb(i)}{cnw(ib(i))} \right) \end{aligned} \tag{26}$$

In equation 26, $legnpp = 0, \ldots, 1$ is a factor which stands for the fraction of net primary productivity that is provided by legumes in a given biome ib. The values for $legnpp$ are given in table 3. A fraction of 0.3 of the NPP of legumes is assumed to be supported by nitrogen fixed by symbionts. The second line is the correction of N_2 fixation due to the actual N demand. In the third line of equation (26) npp stands for net primary productivity, h means herbaceous, w means woody, a above ground, b below ground, cnh and cnw are standard C/N ratios for herbaceous and woody material for a given biome ib.
N fixation by *Azospirillum* symbionts in C4 grasses and cereals:

$$\begin{aligned} azonf(i) &= c4npp(i(i)) \cdot 0.03 \\ &\quad \cdot \frac{resn0(i)}{resn(i)} \end{aligned}$$

$$\cdot \frac{nppha(i) + npphb(i)}{cnh(ib(i))} \tag{27}$$

Again, $c4npp$ is the fraction of NPP provided by C4 plants of a given biome (see table 3).

N_2 fixation by non–symbiontic organisms like actinomycetes, blue–green algae, symbiontic blue–green algae in lichens, and others: NCIM assumes that this flux will be most effective on poor soils, expressed by the sand fraction of the soil. In addition, this fixation flux is proportional to the respiration flux of microorganisms $mircf$:

$$actnf(i) = 0.01 \cdot mircf(i) \cdot sand(i) \tag{28}$$

The respiration of microorganisms in NCIM depends on the amount of decomposable material in the litter and soil. This depends on the net primary productivity and therefore indirectly on the atmospheric CO_2 concentration. Hence an indirect influence of the rising atmospheric CO_2 concentration on the N_2 fixers from equation (28) is observed in NCIM (see also Hungate *et al.* 1999).

2.2 Model experiments

In order to investigate the principal carbon–nitrogen interaction mechanisms at the global scale we tested the behavior of NCIM's carbon and nitrogen pools under different conditions of atmospheric carbon dioxide and nitrogen supply or loss. We carried out five model experiments (see table 7): constant atmospheric CO_2 with nitrogen input and no losses (nitrogen surplus), and rising atmospheric CO_2 with 4 different levels of nitrogen input, losses, and anthropogenic deposition. The experiments were carried out for the periods 1860 (preindustrial) to 2002 and 2002 to 2100, exept experiment five, which was only run for the first period, due to the lack of data of the future anthropogenic nitrogen deposition. The explicit configuration of these model experiments is found in table 7.

We used long–term mean monthly climate data for the modelling periods from 1860 to 2100 (Leemans & Cramer 1991). We excluded monthly climate anomalies to obtain a clear view of the interactions between the carbon and nitrogen systems without the influence of specific weather events.

The state of the model pools at the beginning of a modeling period is most critical for the reliability of transient model results which were analized in this study. Therefore, we applied a spin–up procedure, which brings the model pools into a dynamic equilibrium with the changing driving forces at the beginning of the model run, i.e. in the year 1860.

The first period of the spin–up procedure took 6 000 model years and ended in 1400 AD. During this period, the C/N ratios of the allocated plant material were set to standard values (see table 3) for woody and herbaceous materials for each biome and were kept constant. All nitrogen and carbon pools of the model were filled to a level which was in equilibrium with the standard C/N ratios of the phytomass pools. The respective model configuration during these first spin–up precedures was set in each model experiment according to the specifications given in table 7. From the model year 1400 to 1860 a "relaxing" period in the model spin–up procedure followed. In this period, C/N ratios of allocated material which were former fixed were now re–calculated at the beginning of each time step from the respective pools so that the organismic, litter, and soil pools could adjust to a dynamic equilibrium. This period was also necessary to achieve a dynamic equilibrium with the already slightly rising atmospheric CO_2 concentration (Barnola *et al.* 1995).

For the two modelling periods, we analyzed changes of NCIM's carbon and nitrogen pools for modifications of their storage capacities, for the five model configurations. For this purpose, we turned on and off the fluxes nitrogen fixation, denitrification, leaching, anthropogenic deposition, together with a constant or rising atmospheric CO_2 concentration. The configuration of these five model experiments is found in table 7.

3 Results and Discussion

3.1 Model validation and regional results for 2002

The primary aim of this paper is to investigate the change in the storage capacity of terrestrial nitrogen and carbon pools during transient model runs influenced by the changing atmospheric CO_2 concentration and its effects on the biospheric carbon gain and loss. For the validation of the model behavior at a given time we used results of our model experiment 4 (see table 7) for the model year 2002 for comparison with experimental results and results from other model simulations. The data are found in the tables 4 – 6.

In table 4 we compare the mean phytomass carbon pools for four major biomes as predicted by NCIM with respective compilations of stand observations by Cannell (1982) and Luyssaert *et al.* (2007). Considering the, compared with the number of experimental sites, high number of grid elements in NCIM, and the high standard deviation of the mean values, the model results fit into the ranges of experimental data. The model result for tropical rain forests of 29.1 ± 5.2 kg·m^{-2} is higher than the the value of 22.9 ± 7.1 kg·m^{-2} by Cannell (1982), although within the range of their standard deviations. Luyssaert *et al.* (2007) give an even lower value of 14.3 kg·m^{-2}. Sarmiento *et al.* (2005) state that tropical forest accumulates one of the largest biomasses among terrestrial ecosystems, but its precise amount and patterns of spatial variation are still imperfectly known. Another reason for lower values of observations may be that as a rule observations rarely include the herbaceous understory and the epiphytes. Both can contribute a considerable portion to the total phytomass, especially of low–biomass stands on poor soils (Golley *et al.* 1971; Edwards *et al.* 1977; Tanner *et al.* 1977). Moreover, the below–ground portion of the phytomass is often underestimated in tropical forests. It contributes to the total stand phytomass at least about 20% (Sarmiento *et al.* 2005) and up to 80% on very poor soils (Klinge 1975; Klinge *et al.* 1978).

We compared NCIM's mean soil organic carbon pools (SOC) and their C/N ratios for seven different biomes with respective mean values that we calculated from the worldwide organic carbon and nitrogen database (Zinke *et al.* 1984). The results are found in table 5. The mediterran woods and shrubland biome has the lowest SOC values from NCIM, 10.5 ± 4.1 kg·m^{-2}, as well as from the database, 7.5 ± 6.6 kg·m^{-2}. The tropical lowland rain forest and the steppe and grassland biomes are also low in SOC in the range of 9–12 kg·m^{-2} carbon for either data source. The highest means in NCIM and in the database were found for the boreal evergreen forest biome. Its SOC pools range from 16–22 kg·m^{-2}. The high standard deviations of the means from the data base for all seven biomes, which lie for most of the biomes between 70% and 98% of the means, is remarcable. NCIM reproduces the order of mangitude of the standard deviatios. The highest values of the standard deviation of 195% (Zinke) and 148% (NCIM) of the means were found in the boreal evergreen forest biome, due to the heterogeneity of the soils in this biome. At a first sight NCIM seems to underestimate SOC in the boreal forest biome. But it must be taken in account that the representation of soil types is different in NCIM and in the database: A majority of the database sites originates from regions which are dominated by fertile Cambisols, whereas infertile Podzols occupy a great part of the boreal zone at the global view.

Maps showing NCIM's global distribution of the nitrogen content in various pools are found in the figures 3 – 5.

NCIM's global distribution of phytomass nitrogen is shown in figure 3. The highest values up to 300 g·m^{-2} occur in tropical rain forests. NCIM reproduces the lower values of dry forests, woodlands, and savannas. In South America, the Caatinga shrublands of north–eastern Brazil and the savannas of Campos Cerrados from western Piaui through central Brazil to the northeast of Paraguay are characterized by 30–50 g·m^{-2} nitrogen. Even rather small savanna islands within the rain forest, for example the Sierra do Cachimbó in southern Pará, are reproduced by NCIM.

South of the Campo Cerrado region, subtropical forest is found from Minas Gerais through Paraná and eastern Paraguay with values from 150 to 250 g·m^{-2}. The dry forests of the Gran Chaco in western Paraguay and northwest Argentina show 50–150 g·m^{-2}. The Pampa steppes and the Patagonian semi–deserts have values less than 30 g·m^{-2}. Temperate forests (eastern and southeastern USA, Europe, eastern China, Japan) lie between 50 and 100 g·m^{-2}. The rough pattern of the nitrogen distribution and the total range of values from NCIM are not very different from other recent model results (a respective map by the DyN–LPJ model is found in Xu–Ri and Prentice 2008), but NCIM reproduces the influences of the vegetation type and the soil quality on phytomass nitrogen in more detail.

Figure 4 shows the global distribution of NCIM's total soil nitrogen. The soil N distribution is different from that of N in phytomass. The highest values of soil N occur in regions with organic soils (Histosols) of the boreal and subpolar zones but also of tropical bogs and tropical highlands. Distinct high nitrogen levels above 1 250 g·m^{-2} are typical for the regions south of the Hudson Bay, the lower Mackenzie region, northern Finland, and the central Ob–Irtysch region of Siberia. High values of soil N between 800 and above 1 000 g·m^{-2} also occur in humus–rich soils (Chernozems, Kastanozems) of the russian steppes, the prairies of midwest North America, the pampas of Argentina, northwestern China and southeastern Siberia, and others. In contrast to results from DyN–LPJ (Xu–Ri & Prentice 2008) of up to 1 800 g·m^{-2}, NCIM predicts moderate values (250–750 g·m^{-2}) for arctic tundra regions.

The distribution of nitrogen in the biomass of soil organisms as shown in figure 5 differs from total soil N. Highest values are found in humid arctic regions as well as in humid highlands of lower latitudes. Elevated values are also found in regions with fertile soils as for example the brown forest soils (Cambisols).

A comparison of the nitrogen storage in the major terrestrial compartments as modelled by NCIM with results from other models or global estimates is found in table 6. There is ample variation in the prediction of the nitrogen content of the major terrestrial compartments. Total phytomass nitrogen in NCIM is about 10.5 Pg. This is close to the result by JSBACH (Parida *et al.* 2009) of about 12.3 Pg. Other models suggest lower values of 3.8 Pg (O–CN, Zaehle *et al.* 2009b/c) and of 5.3 Pg (DyN-LPJ, Xu–Ri *et al.* 2008).

The litter nitrogen of NCIM is only about 1.5 Pg and thus the lowest of all compared models, which lie in the range of 2–4.6 Pg. Older simulations are as high as 10 Pg (Davidson 1994). One reason for the low value of NCIM is that NCIM considers soil organisms with their narrow C/N to belong to the soil compartment.

NCIM's organic soil nitrogen is the largest biospheric nitrogen pool with about 81.4 Pg. The range of other estimates by recent models is from 67 (DyN-LPJ) to 250 (JSBACH) Very high estimates above 150 Pg N would require either very high soil carbon pools or unrealistic (FAO–Unesco 1977 ff.) wide C/N in soil.

NCIM predicts high values for total inorganic soil nitrogen of about 17 Pg. The available nitrogen avn, i.e the fraction dissolved in soil water, on the other hand is with about 0.3 Pg very low. The major quantity of the inorganic nitrogen is adsorbed to clay and humus. The adsorption of inorganic nitrogen immobilizes the N compounds and reduces losses by leaching. This behavior of NCIM is extremely important for the model predictions, and it is supported by recent field studies: In temperate rainforest soils of volcanic origin in Chile it could be shown, that despite high nitrogen turnover rates, loss of bioavailable nitrogen is minimal in these ecosystems (Huygens *et al.* 2008). Recent research into the nitrogen dynamics in soil show a shift of available nitrogen compounds towards NH_4^+ under elevated CO_2 in grasslands which may even further increase the N retention (Müller *et al.* 2009).

3.2 Transient model results

The change in the global carbon and nitrogen storage in the terrestrial biospheric pools in the two modeling periods 1860–2002 and 2002–2100 is found in tables 8 and 9.

3.2.1 Constant atmospheric CO_2, nitrogen input, and no losses (N surplus)

We used a constant atmospheric CO_2 concentration at the preindustrial level of 280.68 ppm throughout the two periods. We activated biological N_2 fixation in the model. Leaching and denitrification were switched off, so that the biosphere stored the imported nitrogen, and became over–supplied with nitrogen.

The total nitrogen content of the terrestrial biosphere increased by $+37.0$ Pg in the first period 1860 to 2002, and another $+26.7$ Pg up to 2100. Because of constant atmospheric CO_2, carbon storage in the biosphere was only influenced by the increasing nitrogen availability. In the first period, total carbon increased slightly by $+13.3$ Pg. In contrast, it was reduced in the second period by -20.8

Pg. These changes of the total carbon storage were the result of diverse effects in living biomass and in soil. While the organismic carbon in plants and soil microorganisms increased $+40.5$ Pg in the first and $+6.6$ Pg in the second period, the amount of carbon in non organismic soil pools was reduced by -27.2 Pg (first period) and -27.4 Pg (second period) by the enhanced decomposition of humus and especially of the nitrogen free lignin residuals. The major portion of the additionally bound N was stored in the mobile soil pool, i.e. the available and adsorbed buffer N ($+30.5$ Pg respective $+24.3$ Pg). The excess nitrogen thus provided the nitrogen necessary to mineralize litter and soil pools which are poor in N compared with the requirements of microorganisms. There is experimental evidence for these effects of long–term nitrogen overfertilization from fertilization experiments in natural tundra ecosystems (Mack *et al.* 2004).

3.2.2 Rising atmospheric CO_2 and constant biospheric nitrogen (CO_2 induced N deficiency)

In this model experiment, we assumed that the CO_2 concentration of the atmosphere raised as observed respectively predicted (second period), while the nitrogen fluxes N_2 fixation, denitrification, and leaching were switched off, i.e. the total amount of nitrogen in the biosphere was constant throughout the two modeling periods.

In the period 1860 to 2002, the total amount of carbon stored in the terrestrial biosphere increased by $+108.2$ Pg. The majority remained in the living phytomass and in the biomass of soil microorganisms, so that the storage in the organismic biomass was about 66%. 34% were stored in the non organismic pools of litter and soil organic carbon, mainly in the nitrogen–free lignin residuals.

While the total nitrogen content of the terrestrial biosphere did not change in this experiment, there was a redistribution of nitrogen among the biospheric pools. Increases in the nitrogen content were observed in the pools of litter, soil, and biomass of microorganisms, while structural nitrogen in plants increased a little less. Organismic N increased by $+0.8$ Pg, non organismic N by $+0.4$ Pg. A source for this nitrogen was the mobile reserve nitrogen in plants (-0.2 Pg), so that a moderate increase of total plant nitrogen of only 2% resulted. The main sources however were the mobile pools of the soil, available and adsorbed nitrogen (-1.0 Pg). This model result is supported by recent empirical evidence (Müller *et al.* 2009). We conclude that the increased carbon storage, as a consequence of the rising atmospheric CO_2, favors nitrogen storage in the organismic and non organismic fractions, to the debit of mobile plant and soil nitrogen. Plants and soil organisms may, as a consequence of less available mobile N, become more susceptible to transient changes in the overall nitrogen availability. Ecosystems with small reserve nitrogen pools in plants and in poor soils, for example grasslands and savannas, may be limited very early after experimental application of elevated CO_2 (Reich *et al.* 2006a). In fertile soils, the mobile nitrogen pools in the soil may even have higher nitrogen capacity than traditionally expected as even organic N containing monomers probably can be utilized by both, microorganisms and plants (Schimel & Bennett 2004).

For the period 2002 to 2100, a further increase of the atmospheric CO_2 concentration to 875 ppm (mean of 730–1020 ppm (Meehl *et al.* 2007)) is predicted[3]. For again a constant amount of N in the biosphere (N_2 fixation, denitrification, and leaching switched off), the picture of the first period is confirmed. $+167.2$ Pg of C are additionally stored in the terrestrial biosphere, 63% of this amount in the organismic pools and 37% in the non organismic pools in litter and soil. Further shifts from plant reserve N (-0.4 Pg) and mainly from available and adsorbed N in soil (-1.3 Pg) to structural N in plants and microorganisms and to non organismic pools in litter and soil occur. The preference of organismic N pools is less marked than in the first period.

The mean[4] C/N in leaves shifted from 24.8 (1860) over 25.5 (2002) to 26.9 (2100); the mean values for C/N in wood were 144.3, 147.8 and 155.9. The soil C/N widens from 16.5 (1860) over 16.9 (2002) to 17.6 (2100). This experiment strongly underlines the high importance of mobile, in particular adsorbed nitrogen in soils as main source for additional nitrogen requirements caused by increasing carbon pools as a consequence of the rising atmospheric CO_2. This is especially critical in ecosystems dominated by soils with low exchange capacity for N. Recent field studies support this model result (Huygens *et al.* 2008; Müller *et al.* 2009).

3.2.3 Rising atmospheric CO_2 and nitrogen losses (enhanced N deficiency)

We switched on nitrogen leaching while the atmospheric CO_2 was rising, in order to induce enhanced nitrogen deficiency in the terrestrial biosphere. This caused total losses from the terrestrial biosphere of -10.2 Pg nitrogen in the period 1860 to 2002 and -3.1 Pg in the period 2002 to 2100. The losses occurred in all terres-

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[3] We calculated annual values from a function fitted to the Mauna Loa Data and 875 ppm in 2100 of the form: $f(x) = a + b \cdot exp(c \cdot (x - d))$ with x being the calendar year (AD) and the parameters: $a = 262.31$, $b = 0.01535$, $c = 0.017389$, $d = 1490.76$.

[4] Global area–weighted means

trial nitrogen pools, but were strongest for available and adsorbed nitrogen in the soil: -8.0 Pg N in the first and -1.9 Pg N in the second period. The lower losses in the second period were due to the lower concentrations of mobile nitrogen in soil, which reduced the leaching flux. Considerable but much lower reduction of mobile plant N was also found (-0.5 Pg respectively -0.4 Pg N). The rising atmospheric CO_2 concentration led to only moderate sequestration of carbon in the terrestrial biosphere, most of which was stored in the phytomass. The global mean C/N of leaves changed from 24.8 in 1860 to 26.2 in 2002, and further to 28.1 in 2100. The C/N for wood changed from 144.3 (1860) to 151.0 (2002) and then to 161.7 in 2100. The biomass of soil microorganisms was considerably reduced by 12% in the period 1860 to 2002 and another 2.5% in 2002 to 2100, as a consequence of the lower nitrogen content in litter and soil: the mean C/N of litter changed from 45.6 to 50.8 and of soil from 16.5 to 18.6 from 1860 to 2002, and further to 2100 to 55.9 (litter) and 19.3 (soil).

We found an accumulation of carbon in lignin derivatives in soils ($+12.3$ Pg C), but minor carbon losses from humic substances (-0.2 Pg C) due to a reduced production of humic substances (-5.7%) by soil organisms. This is in agreement with earlier studies (Melillo *et al.* 1991; Norby *et al.* 2001), which found a general reduction of the activity of soil organisms as a consequence of wider C/N ratios in litter.

The rising atmospheric CO_2 concentration used in this experiment caused a higher carbon storage in plants due to the fertilization effect of atmospheric CO_2. This induced additional nitrogen demands in plants, litter and soil. On the other hand, N losses from leaching, which, in this experiment, were not compensated by nitrogen inputs into the biosphere, mean less N supply. The mobile N pools, i.e. the reserve N in plants and the available and adsorbed N in the soil, became the major providers for additional N requirements, which result from the rising atmospheric CO_2 concentration. In principle, plants and soil organisms compete for available nitrogen. However, in the long term plants have an advantage over microorganisms in the acquisition of nitrogen, because the turnover time of nitrogen in plant material is much longer than that of microorganismic biomass, which makes microorganismic N more susceptible to losses by redistribution (Huygens *et al.* 2008).

3.2.4 Rising atmospheric CO_2, nitrogen input, and nitrogen losses (full C/N feedback)

A forth experiment was performed that combined all natural processes which are relevant for the N and C balance of the terrestrial biosphere: Rising CO_2 concentration of the atmosphere, symbiontic and non–symbiontic nitrogen fixation, denitrification, and leaching of soluble nitrogen compounds from soil.

Using this model configuration the total carbon content of the terrestrial biosphere increased by $+160.0$ Pg C in the first modelling period (1860 to 2002). This amount of carbon bound in the biosphere is similar to what was expected from observations ("missing sink", see Introduction). Another $+280.1$ Pg C were sequestered in the shorter second period (2002 to 2100).

Thus much more carbon was sequestered in both periods than in the two model experiments 1 (nitrogen fixation, no losses) and 2 (rising CO_2) together. Rising atmospheric CO_2 and the minor nitrogen fluxes in combination induced a strong fertilizing feedback in the terrestrial biosphere, which was much higher than the sum of the individual influences.

The global distribution pattern of the additionally sequestered carbon is found in figure 6. The tropical and subtropical humid forests store much of the carbon with values of more than 2 000 $g{\cdot}m^{-2}$. Forested regions of the temperate and boreal zones stored between 1 500 and 2 000 $g{\cdot}m^{-2}$.

We found the highest carbon storage in plants and soil organisms, which accumulated $+126.8$ Pg C in the first period. The majority of this, i.e. $+102.1$ Pg, was stored in the phytomass, 95% of this in woody material. Pepper *et al.* (2005) found that woody biomass is a preferred compartment for carbon storage due to its wide C/N and, therefore, low N requirements. Figure 7 shows the global distribution of the additional phytomass carbon. It resembles the distribution of total carbon in figure 6, since phytomass is the major compartment of additional carbon storage.

The biomass carbon of soil organisms increased by $+24.7$ Pg. Its global distribution is found in figure 8. A great part of the increase is in tropical humid regions, but the boreal and some subpolar regions as well as savannas and some steppes contribute considerably.

The carbon pools in lignin residuals and humic substances increased by only $+25.8$ Pg. This additional carbon stored in the non–organismic part of the soil is shown in figure 9. Rainforests seem to contribute little. Even carbon losses occur, which are the result of the increasing decomposition of lignin due to the increasing availability of nitrogen from N_2 fixation. The major soils for sequestration of additional soil carbon are found in boreal and humid subpolar regions. There is also some increase in soil carbon in regions where decomposition is limited by climatic influences rather than by nitrogen availability.

Litter carbon increased by $+7.4$ Pg, so that litter and non–organismic soil pools together store $+33.2$ Pg. Organismic pools thus dominate the storage of additional carbon. This seems to be characteristic for conditions in which nitrogen is not limiting the carbon sequestration.

In the second period, 2002–2100, a slightly different picture was found. $+181.6$ Pg of the total $+280.1$ Pg carbon were stored in the living phytomass, 97% of this amount in woody material. $+15.8$ Pg in soil organisms, $+71.9$ Pg in lignins and humic substances, and $+10.8$ Pg in litter. The higher storage of carbon in soil and the relatively lower increase of organismic biomass may be interpreted as a consequence of a beginning nitrogen limitation of carbon mineralization in soil (McMurtrie *et al.* 2001).

The net nitrogen content of the terrestrial biosphere increased by $+11.0$ Pg in the first and $+8.5$ Pg in the second period. Hungate *et al.* (2003) estimated a likely range of $+1.2$ to $+6.1$ Pg N for biospheric N accumulation until 2100, based on simple mass balance and stoichometry considerations. Multiple previous model studies (cited at Hungate *et al.* 2003) which did not or not adequately treat the C/N stoichometry of real ecosystems yield nitrogen requirements from $+7.7$ to $+37.5$ Pg for the period up to 2100. NCIM's result is in the lower range of these studies, which were based on an equal distribution of the sequestered carbon between trees and soil. NCIM in contrast produces a distribution of the sequestered carbon between the phytomass and the litter–soil complex of 1.8 : 1, which may be responsible for lower N demands. Nevertheless NCIM's value is above even the upper limit for N accumulation calculated by Hungate *et al.* (2003). This higher accumulation in NCIM is mainly based on the biological nitrogen fixation by free living organisms, namely cyanobacteria, and symbiontic cyanobacteria in lichens and mosses as described by equation (28). The global distribution of the additionally stored nitrogen calculated by NCIM is found in figure 10.

The increase of the biospheric N content is a consequence of the relatively higher promotion of N_2 fixation compared to losses of N from the biosphere. The N_2 fixation flux by symbiontic and free living microorganisms grew about 18% in the first and another 15% in the second period. This is in the lower range of earlier assumptions by Hungate *et al.* (2003) of 10%–45% with CO_2 doubling. The less relative increase in the biological nitrogen fixation in the second period is due to the less increase in the biomass of soil organisms of $+24.7$ Pg C in the first and $+15.8$ Pg C in the second period as discussed above, compare also equations (14) and (28).

The C/N ratios of the biospheric compartments remained considerably well balanced in this experiment. From 1860 to 2002, the global mean C/N of leaves sank from 24.6 to 24.3, that of wood from 144.2 to 142.8, that of litter from 45.2 to 43.5, the soil C/N from 16.5 to 15.4. In the second period from 2002 to 2100, there were no changes in the global mean C/N ratios of the phytomass and of litter, while that of soil sank slightly from 15.4 to 15.2. On a global view there were no nitrogen deficiencies caused by the additionally bound carbon due to the rising atmospheric CO_2. In NCIM the changed processes of nitrogen turnover together with the enhanced biological nitrogen fixation provided the amount of nitrogen which was necessary to keep the C/N stable, although the carbon pools increased because of the rising atmospheric CO_2. This finding is in contrast to earlier results which sometimes found a limitation of carbon sequestration by soil fertility under elevated CO_2 (Oren *et al.* 2001). During the modelling period of 240 years, we did not see at the global scale the sometimes apprehended increase of C/N ratios in plant materials as a consequence of the rising atmospheric CO_2 concentration (Hungate 1999). At the global scale nitrogen deficiency in plant material occurred only under conditions of strong N limitation, as generated in experiment 3. The reduction of the nitrogen content in plants, as observed in FACE experiments under elevated CO_2 (Ellsworth *et al.* 2004), is probably responsible for the reduction of the photosynthetic carboxylation capacity often observed in these experiments. But it is unclear if such widening of the C/N ratio would also occur along with the, compared to FACE experiments relatively slow, rise of atmospheric CO_2 under natural conditions, which would give N_2 fixing organisms time to compensate for the N deficiency in the ecosystem. Pepper *et al.* (2007) emphasize in a model based sensitivity study the great importance to distinguish between ecosystem processes which are important on the short term, and those important on the long term, as for example carbon allocation to tree root exudates that may influence N_2 fixation. From their model experiments and using a parameterization for a N–limited Norway spruce stand of northern Sweden, they conclude that N_2 fixation has much potential to enhance the long term CO_2 response.

3.2.5 Rising atmospheric CO_2, nitrogen input, losses, and anthropogenic N deposition (anthopogenic N deposition)

Recently the role of the anthropogenic nitrogen deposition for the carbon sequestration has been discussed (Galloway *et al.* 2004; Pregitzer *et al.* 2004; Churkina *et al.* 2007; Magnani *et al.* 2007; Schrijver *et al.* 2008). We reran NCIM's experiment 4 for the modeling period 1860–2002 using a nitrogen deposition scheme developed by Nevison *et al.* (1996). At the global scale the effects of this additional N input into the terrestrial biosphere, in comparison to experiment 4, were very limited. The total carbon content increased only $+1.3$ Pg more than in experiment 4. $+0.9$ Pg of this additional storage was in the biomass of soil microorganisms. The total nitrogen content grew $+0.7$ Pg more than in experiment 4. The N_2 fixation was somewhat reduced and the leaching was higher than in the original experiment. Overall, the effects were small. Other studies using the model Biome-BGC (Running & Hunt 1993) found similar low influences of nitrogen deposition on carbon sequestration in undisturbed ecosystems (Churkina *et al.* 2007). These results do not necessarily contradict other model results which showed stronger effects of nitrogen deposition, especially in boreal systems. There are experimental and modelling results from different biomes which indicate that N_2 fixation is frequently higher than the anthropogenic nitrogen deposition (Lamarque *et al.* 2005; Churkina *et al.* 2007; Reay *et al.* 2008). The nitrogen fixation prevents nitrogen deficiency with rising atmospheric CO_2. Therefore, additional nitrogen input by deposition leads to higher losses and reduction of the biological nitrogen fixation rather than to increasing productivity in NCIM. We have empirical evidence in tropical rain forests that nitrogen deposition may reduce the nitrogen fixation flux (Cusack *et al.* 2009). In any case, the correct prediction of the N_2 fixation is crucial for a reliable prediction of the effects of nitrogen deposition.

3.3 General discussion

The results presented here are characterized by several special features. Rising atmospheric CO_2 in NCIM does not cause strong nitrogen limitation of biospheric processes at the global scale, if all relevant processes of nitrogen turnover and nitrogen input and output are active in a model run. In contrast, nitrogen limitation occurs if the biological nitrogen fixation is turned off, especially if CO_2 is rising at the same time. If, on the other side, the biosphere is oversupplied with nitrogen by turning off losses while biological nitrogen fixation is active, even losses from soil carbon may occur due to the enhanced activity of soil organisms.

This strongly underlines the great importance of biological nitrogen fixation for the biospheric nitrogen supply. Although the fluxes of nitrogen fixation are minor fluxes compared with the major fluxes nitrogen mineralization, nitrogen uptake by plants, and nitrogen allocation, they contribute considerably, in the long run, to the compensation of the N deficiency from the enhanced carbon assimilation caused by the rising CO_2.

Recent models which couple the carbon and nitrogen cycles but do not treat the biological nitrogen fixation dynamically as a function of the vegetation nitrogen demand, show nitrogen limitation at the global scale, especially if nitrogen losses by leaching and denitrification are included (Zaehle *et al.* 2010a). We get similar results in our experiment 3 using a similar model configuration (see section 3.2.3).

Despite its importance little is known about the biological fixation fluxes in natural ecosystems. Estimates even in recent publications (Galloway *et al.* 2004) still partly rest on rather old calculations (Stedman & Shetter 1983). The mechanistic prediction of symbiontic nitrogen fixation, for example, requires a reliable description of the global distribution of the symbionts' host plants, their density distribution in the respective vegetation units, the type and number of root nodules, and the activity of N_2 fixing enzyme systems in the nodules. The change of all these parameters under a varying atmospheric composition, climate, and competition must be predicted. There is still a way to go in order to be able to do this, but it is clear, from our model results and from empirical studies (e.g. Reich *et al.* 2006a; Pepper *et al.* 2007), that predicting these processes must have very high priority. In particular the contribution of free living organisms such as cyanobacteria, also occuring symbiontically in lichens and mosses, has been considered low. But evidence exists that lichens and mosses are important nitrogen fixers which contribute considerably to the nitrogen balance in boreal systems (Henriksson & Simu 1971; Crittenden 1975; Weiss *et al.* 2007; Menge & Hedin 2009). For tropical forests it could be shown that mosses and lichens and free living soil organisms provide large inputs of nitrogen into the forest ecosystem, but the nitrogen fixation is likely to be sensitive to increases in N deposition in tropical regions (Cusack *et al.* 2009). This interaction of biological nitrogen fixation and nitrogen inputs by anthropogenic deposition is responsible in NCIM for the small effects of anthropogenic deposition on the carbon sequestration. Other models which do not treat the biological nitrogen fixation dynamically as a function of vegetation nitrogen demand show stronger effects (Zaehle & Friend 2010b; Zaehle *et al.* 2010c).

NCIM calculates considerable N_2 fixation rates in boreal systems and in other ecosystems because of the activity of free–living (Macgregor & Johnson 1971) and symbiontic cyanobacteria in lichens (Forman 1975; Crittenden & Kershaw 1978; Zackrisson *et al.* 2004; Weiss *et al.* 2005; Hodkinson *et al.* 2008) and on mosses (DeLuca *et al.* 2002), which are common on trees and poor (podzolic) soils (Esseen *et al.* 1996; Kumpula *et al.* 2000; Liu *et al.* 2000; Lehmkuhl 2004).

A second special feature of NCIM is the feedback between the carbon and nitrogen cycles. Several processes in NCIM cause positive feedbacks of the rising atmospheric CO_2 with nitrogen uptake by organisms and with biological nitrogen fixation, and negative feedback with nitrogen losses. The nitrogen uptake by plants depends on the leaf mass which increases with higher CO_2 (see equation(1)). In addition, the uptake by plants is further enhanced by the higher N demand due to reduced pools of reserve nitrogen, which occur as a consequence of more carbon allocation. Higher litter production from elevated CO_2 triggers the production of humic substances by soil organisms and thus increases the buffer capacity for available nitrogen in the soil and reduces leaching (see equations (19)–(24)). The reduced pool of reserve nitrogen in plants enhances the nitrogen fixation by their symbionts (see equations (26)–(27)). The biomass of soil organisms increases by the higher litter production and promotes the respiration of soil organisms (equation (14)) and the nitrogen fixation of free living fixers and cyanobacteria (equation (28)). Higher litter production also enhances net mineralization of soil organic nitrogen and thus losses by denitrification (equation (25)). Churkina *et al.* (2009) in a model study found similar strong synergistic effects between nitrogen input by deposition and rising atmospheric CO_2 on the carbon uptake of land. In NCIM, increasing N_2 fixation takes the role of N input, while deposition may replace biological nitrogen fixation thus causing only limited additional effects.

A third feature of NCIM is the existence of certain pools of nitrogen which serve as reservoirs: The reserve nitrogen in plants, and the buffer pool of available nitrogen in the soil. Both pools can rapidly provide nitrogen to support accelerating processes of carbon binding at the beginning of the vegetation period. Seasonal nitrogen deficiency in plants and soil organisms is thus mitigated or even prevented.

3.4 Empirical evidence

NCIM is based on largely independent carbon and nitrogen cycles with free floating C/N ratios, and a microorganism centred approach to describe litter and soil processes. The structure of NCIM enables a comparison of results to different kinds of independent estimates and observations. Total carbon and nitrogen sequestration by NCIM may be compared to estimates at the global scale, while patterns of responses of different pools of carbon and nitrogen and C/N ratios may be compared to experiments with elevated atmospheric CO_2 concentrations. Still, CO_2 enrichment experiments (open–top chambers and free air carbon enrichment, FACE) are characterized by two features: first they represent the response of one specific system at the respective site. Comparison to NCIM results is therefore most valid for meta–analyses based on several plots. Second the CO_2 enrichment is conducted in a step–increase, which introduces an imbalance in the carbon–nitrogen system. Here long term CO_2 enrichment, which allows the system to compensate partly for this imbalance may be most informative.

At the global scale we find for the period 1860–2002 a carbon sequestration compensating for the missing sink, but only in the fully coupled carbon–nitrogen experiment with NCIM. This fertilization feedback was stronger than the sum of separate influences of high nitrogen supply and rising atmospheric CO_2. For the period 2002–2100 NCIM predicts an ongoing carbon sequestration on the low end of the expected range, along with an increase of ecosystem N content which was higher than the range calculated by simple mass balance and stoichiometric calculations (Hungate *et al.* 2003).

Experiments with elevated CO_2 often have indicated a progressive nitrogen limitation which could severely constrain a CO_2 fertilization effect on the long term. On the other hand there is also evidence for an adaptive response of the ecosystem to ameliorate CO_2 induced nitrogen limitation by additional uptake and redistribution (Luo *et al.* 2006b). In a meta–analysis of 104 studies Luo *et al.* (2006a) found that average C/N ratios are higher by 3% in litter and soil and 11% in plants at elevated relative to ambient CO_2. At the same time additional nitrogen was sequestered in plant and soil pools. In a review on carbon–nitrogen interaction in CO_2 enrichment experiments, Reich *et al.* (2006b) found some evidence for a CO_2 induced enhancement of nitrogen fixation, but also for no response. Therefore they finally concluded that evidence from long–term field studies suggests that both progressive nitrogen limitation under rising CO_2 and a significant interaction between CO_2 and nitrogen are likely to be common in many natural ecosystems, leading to carbon sequestration in the low range anticipated (Reich *et al.* 2006b). Hungate *et al.* (2006) showed for a seven year FACE study that elevated CO_2 caused a substantial redistribution of nitrogen within the ecosystem, from mineral soils to plants.

NCIM reproduces this general pattern of widened C/N ratios in situations of induced nitrogen limitation (model experiments 2 and 3), a substantial redistribution of nitrogen from soil mobile and adsorbed compartments towards structural plant pools (model experiments 2, 3, and 4), and additional nitrogen sequestration under rising CO_2 concentrations (model experiment 4). The fully coupled carbon–nitrogen mode of NCIM does not show a widening of C/N ratios as often observed in FACE and open–top chamber experiments with instantaneous CO_2 enrichment, as a slow rise of CO_2 in the model experiments provides time for N_2 fixers to compensate for the nitrogen requirements of the additionally bound carbon. Nevertheless, the carbon sequestration predicted by NCIM for the period 2002–2100 is in agreement with the conclusions from empirical evidence by Reich *et al.* (2006b).

3.5 Conclusions

An obvious result of our experiments with NCIM was that the most important processes for carbon sequestration in the terrestrial biosphere, besides the rising atmospheric CO_2, are those of the nitrogen cycle: fixation of atmospheric nitrogen, denitrification, leaching, and redistribution between biospheric pools.

Independent of the present accuracy of the description of these nitrogen processes in NCIM, we draw some basic conclusions from our model experiments from the global point of view:

- Nitrogen fertilization of the biosphere alone, but without the increase of the CO_2 concentration, would result in only minor additional carbon accumulation in plant biomass. In contrast, in NCIM, it led to carbon losses from the soil. Rising CO_2 alone, without consideration of the nitrogen cycle, would bind roughly half of the carbon requested for the missing sink. A complete ensemble of rising atmospheric CO_2 and N_2 fixation, denitrification, and leaching is necessary to achieve the 160 Pg of carbon bound in the terrestrial biosphere between 1860 and 2002 as requested by the missing sink concept.

- Mobile nitrogen pools, namely reserve N in plants and available and adsorbed N in soil, are the primary sources for additional N requirements in less mobile terrestrial pools, as a reaction to elevated CO_2, in NCIM and in observations. Ecosystems with low reserve pools, like grasslands on poor soils, may therefore be limited by nitrogen availability very early after the experimental application of elevated CO_2.

- If nitrogen is not strongly limiting, organismic carbon pools in living plants and soil organisms are the most important targets for sequestration of new carbon, rather than litter and non–organismic soil organic carbon. Enhanced mineralization fluxes limit the net growth of soil organic carbon, especially that of lignin residues. Results from regional experimental studies support this NCIM prediction (Schlesinger & Lichter 2001; Billings & Schaeffer 2004). Using NCIM, we could show that this phenomenon may be important even at the global scale.

- It is indispensable to differentiate in a model the different compartments of nitrogen and carbon in soil, including humic substances, nitrogen–free litter residues, and soil microorganisms, since their behavior is often diverging mutually and from that of the phytomass of plants.

- Progressive nitrogen limitation of carbon sequestration as deduced from some experiments, which used an instantaneous rise of CO_2 (i.e. FACE, open–top chambers, etc.), is not observed in NCIM. We believe that the naturally slow rise of CO_2 used in the model experiments is responsible for this observation. In contrast to a sudden rise, a slow rise of CO_2 provides time for N_2 fixers to compensate for the N requirements of the additionally bound carbon.

The sequestration of about 280 Pg of carbon between 2002 and 2100, as predicted by NCIM, may be considered as a preliminary value, since we did not include climate effects (Thornton *et al.* 2007). But it underlines the importance to understand the carbon and nitrogen systems and their interaction. The inclusion of climate change effects may considerably reduce this future biospheric carbon storage (Friedlingstein *et al.* 2003), although the coupled atmosphere–land–ocean models used for earlier predictions (Cox *et al.* 2000; Dufresne *et al.* 2002) did not yet consider the feedback of carbon and nitrogen processes in the terrestrial biosphere. It will be important to consider the change of the minor nitrogen processes N_2 fixation, denitrification, and leaching under a changing climate to get these feedback mechanisms correctly.

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Table 1: Denominators of arrays, their meaning and ranges used in the description of the Nitrogen Carbon Interaction Model (NCIM).

denominator	meaning	dimension
i	grid element	1,. . .,62 483
im	month	1,. . .,12
is	soil unit	1,. . .,45
ib	biome	1,. . .,31

Table 2: Conversion list of the texture classes provided by the Global Ecosystems Database (Staub & Rosenzweig 1987) into the $sand$ fraction used in NCIM.

texture class	class name	$sand$ fraction
1	coarse	0.8
2	medium	0.5
3	fine	0.3
4	coarse–medium	0.65
5	coarse–fine	0.5
6	medium–fine	0.4
7	coarse–medium–fine	0.5
8	organic	0.0
9	land ice	0.5

Table 3: The 31 biome groups which were aggregated from the 176 vegetation formations after Schmithüsen (1976) and biome related parameters used in NCIM. ib is the respective array denominator. cnh and cnw are standard values for the C/N ratios of herbaceous and woody material. cnw values were derived from an evaluation of hundreds of published analyses (Clüsener–Godt 1989), considering the diameter distribution of stems, the fraction of branches, twigs, bark and roots (Cannell 1982). They were used in NCIM during the first spin–up period and for the calculation of the symbiontic N_2 fixation. $legnpp$ and $c4npp$ are the fractions of net primary productivity provided by legumes and C4 plants. $rcych$ is the part of leaf nitrogen which is recycled to reserve nitrogen $resn$ in plants before leaves are shed.

ib	biome	cnh	cnw	$legnpp$	$c4npp$	$rcych$
1	tropical lowland rain forests	22.	125.	0.25	0.0	0.0
2	tropical lowland dry forests	22.	125.	0.25	0.08	0.0
3	tropical mountain forests	22.	125.	0.10	0.0	0.0
4	tropical savannas	28.	150.	0.25	0.48	0.15
5	tropical paramo woodlands	28.	150.	0.10	0.0	0.25
6	tropical paramo grasslands	28.	150.	0.10	0.0	0.25
7	puna steppes	28.	150.	0.20	0.0	0.25
8	subtropical evergreen forests	30.	217.	0.10	0.05	0.23
9	subtropical deciduous forests	28.	187.	0.10	0.05	0.17
10	subtropical savannas	28.	150.	0.20	0.20	0.25
11	subtropical halophytic formations	28.	150.	0.20	0.20	0.25
12	subtropical steppes and grasslands	28.	150.	0.20	0.20	0.25
13	temperate steppes and grasslands	28.	150.	0.20	0.05	0.25
14	subtropical semi–deserts	28.	150.	0.40	0.03	0.25
15	xeromorphic formations	25.	162.	0.40	0.14	0.25
16	deserts (tropical, subtropical, cold)	28.	150.	0.40	0.03	0.25
17	mediterran sclerophyllous forests	30.	217.	0.10	0.05	0.23
18	mediterran woodlands and shrub formations	30.	217.	0.20	0.15	0.23
19	temperate evergreen forests	30.	217.	0.10	0.05	0.23
20	temperate deciduous forests	28.	187.	0.05	0.0	0.17
21	temperate woodlnds	30.	150.	0.05	0.03	0.05
22	temperate shrub formations	30.	150.	0.05	0.03	0.05
23	cool–temperate bogs	50.	200.	0.0	0.0	0.65
24	boreal evergreen coniferous forests	30.	187.	0.0	0.0	0.45
25	boreal deciduous forests	34.	217.	0.0	0.0	0.23
26	boreal woodlands	35.	217.	0.0	0.0	0.23
27	boreal shrub formations	28.	164.	0.0	0.0	0.17
28	shrub tundras	45.	150.	0.10	0.0	0.65
29	forb tundras	45.	150.	0.20	0.0	0.65
30	azonal formations	22.	125.	0.25	0.08	0.0
31	mangrove	22.	125.	0.25	0.0	0.0

Table 4: Mean carbon pools in the phytomass and their standard deviation for four major forest biomes as predicted by NCIM for the year 2002 (this paper, model experiment 4), in comparison with two compilations of forest data. n for NCIM means number of grid elements used to calculate the mean. n for Cannell (1982) means the number of available data sites (mature stands only). All values in [kg·m^{-2}] carbon.

biome	NCIM	Cannell 1982	Luyssaert *et al.* 2007
tropical rain forests	29.1 ± 5.2 $n = 6\,340$	22.9 ± 7.1 $n = 17$	14.3
temperate deciduous forests	15.1 ± 4.5 $n = 4\,465$	15.4 ± 5.0 $n = 30$	13.4
temperate evergreen forests	16.2 ± 5.0 $n = 543$	22.7 ± 9.3 $n = 20$	19.6
boreal evergreen forests	7.0 ± 2.3 $n = 5\,881$	9.0 ± 4.4 $n = 16$	7.1

Table 5: Mean soil organic carbon pools, their standard deviation, and their C/N ratios as predicted by NCIM (this paper, experiment 4) for different biomes for the year 2002, in comparison with respective values which were calculated from the worldwide organic carbon and nitrogen database (Zinke *et al.* 1984). Biomes with more than 100 values in the database were considered. In NCIM, SOC is the sum of the pools $humc$, $ligc$, and $micc$ (see figure 1). SOC values are carbon [kg·m^{-2}].

biome	NCIM (this paper)		Zinke *et al.* 1984	
	SOC	C/N	SOC	C/N
tropical lowland rain forests	11.9 ± 9.7	14.4	10.5 ± 9.7	14.2
	$n = 5\,365$		$n = 385$	$n = 360$
subtropical steppes and grasslands	11.4 ± 7.9	14.7	9.1 ± 7.8	13.7
	$n = 306$		$n = 156$	$n = 149$
temperate steppes and grasslands	12.2 ± 11.0	14.4	12.4 ± 8.7	15.7
	$n = 3\,847$		$n = 664$	$n = 336$
mediterran woods and shrublands	10.5 ± 4.1	14.2	7.5 ± 6.6	15.3
	$n = 1\,182$		$n = 259$	$n = 258$
temperate deciduous forests	11.3 ± 9.8	16.4	13.0 ± 11.0	20.8
	$n = 4\,465$		$n = 242$	$n = 111$
boreal evergreen forests	16.4 ± 24.3	20.8	21.9 ± 42.6	18.9
	$n = 5\,881$		$n = 145$	$n = 123$
boreal deciduous forests	6.7 ± 8.5	15.7	12.3 ± 12.1	13.2
	$n = 2\,805$		$n = 179$	$n = 141$

Table 6: Nitrogen storage in major terrestrial compartments as modelled by NCIM in experiment 4 (see table 7) for 2002, in comparison with results from some other models. The NCIM results are further subdivided: phn herbaceous phytomass N, pwn woody phytomass N, $resn$ reserve (mobile) N in plants, $humn$ N in humus, $micn$ N in soil organisms, avn available desolved inorganic N in soil, $puffn$ inorganic N adsorbed to clay and humus minerals. The C/N ratios from NCIM are means for the year 2002 and were calculated on the basis of free–floating pool–ratios since the model year 1400 AD. The C/N ratio for total soil includes the organic and inorganic soil fractions and the nitrogen–free lignin compounds.

all in [Pg] N	NCIM (this paper)		C/N	JSBACH[8]	O–CN[9]	C/N	DyN–LPJ[7]	other simulations	other models[6]
vege-tation	phn	1.3	24.3						
	pwn	7.4	142.8						
	$resn$	1.8							
	total	10.5		12.3	3.8	140	5.3	10[1]	10–16
litter		1.5	43.5	2.1			4.6	10[2]	
soil organic	$humn$	66.2	15.1		litter and soil:			70[1]	
	$micn$	15.2	5.8					95[3]	
	total	81.4		250.1	101	12.8	67	133–140(100cm)[4]	70–820
			total soil: 15.5					63–67(30cm)[4]	
								92–117[5]	
soil inorganic	avn	0.3			0.3				
	$puffn$	16.7							
	total	17.0		2.8			0.94		25

[1] McElroy *et al.* 1976, 1983

[2] Davidson 1994

[3] Post *et al.* 1985

[4] Batjes 1996, 1997

[5] Zinke *et al.* 1984

[6] from Lin *et al.* 2000

[7] Xu–Ri *et al.* 2008

[8] Parida *et al.* 2009

[9] Zaehle *et al.* 2010b; Zaehle *et al.* 2010c

Table 7: Configuration of the five model experiments with the Nitrogen Carbon Interaction Model (NCIM) in the two periods 1860–2002 and 2002–2100. CO_2 means atmospheric concentration of carbon dioxide. Rising refers to the measured (Keeling & Whorf 2005) or predicted (Meehl *et al.* 2007) concentration change for the two periods. Constant means the preindustrial concentration throughout the two periods. N_2 fixation means the processes of fixation of atmospheric nitrogen by symbiontic or free living microorganisms. Denitrification is the production of gaseous compounds like N_2 and N_2O by microbial processes in litter and soil. Leaching is the loss of soluble nitrogen compounds to groundwater and water outfalls. The relevant process descriptions in the model may either be activated (on) of deactivated (off) on grid element level.

Experiment	CO_2	N_2 fixation	denitrification	leaching	deposition
1 (n_sat)	constant	on	off	off	off
2 (c_only)	rising	off	off	off	off
3 (cn−)	rising	off	off	on	off
4 (cn_full)	rising	on	on	on	off
5 (cn_full_d)	rising	on	on	on	on

Table 8: Change of the total carbon and nitrogen storage in the terrestrial biospheric pools in the two modeling periods 1860–2002 and 2002–2100. For the configuration of experiments 1 through 5 see table 7. The figures give the change of the storage between the beginning and the end of either period. Negative values mean decrease of storage. Petagrams [Pg] means 10^{15}g.

	1860–2002		2002–2100	
Experiment	total C [Pg]	total N [Pg]	total C [Pg]	total N [Pg]
1 (n_sat)	+13.3	+37.0	−20.8	+26.7
2 (c_only)	+108.2	±0.0	+167.2	±0.0
3 (cn−)	+52.2	−10.2	+72.9	−3.1
4 (cn_full)	+160.0	+11.0	+280.1	+8.5
5 (cn_full_d)	+161.3	+11.7	–	–

Table 9: Change of the storage of carbon and nitrogen in the compartments of the terrestrial biosphere (groups of pools) in the modeling periods 1860–2002 (upper table) and 2002–2100 (lower table). For the configuration of experiments 1 through 5 see table 7. Organismic refers to plants and soil microorganisms, non organismic includes litter and soil organic substance excluding microorganisms, plant mobile is mobile N compounds in plants, soil mobile includes soluble and adsorbed N compounds in soil. Petagrams [Pg] means 10^{15}g.

1860–2002

Experiment	organismic C [Pg]	organismic N [Pg]	non organismic C [Pg]	non organismic N [Pg]	plant mobile N [Pg]	soil mobile N [Pg]
1 (n_sat)	+40.5	+5.7	−27.2	+0.6	+0.2	+30.5
2 (c_only)	+71.8	+0.8	+36.4	+0.4	−0.2	−1.0
3 (cn−)	+35.3	−1.5	+16.9	−0.2	−0.5	−8.0
4 (cn_full)	+126.8	+5.6	+33.2	+1.1	+0.2	+4.2
5 (cn_full_d)	+128.1	+5.8	+33.2	+1.1	+0.2	+4.7

2002–2100

Experiment	organismic C [Pg]	organismic N [Pg]	non organismic C [Pg]	non organismic N [Pg]	plant mobile N [Pg]	soil mobile N [Pg]
1 (n_sat)	+6.6	+1.9	−27.4	+0.5	+0.05	+24.3
2 (c_only)	+105.0	+0.9	+62.2	+0.8	−0.4	−1.3
3 (cn−)	+55.6	−0.4	+17.3	−0.4	−0.4	−1.9
4 (cn_full)	+197.4	+4.2	+82.7	+1.9	+0.09	+2.3

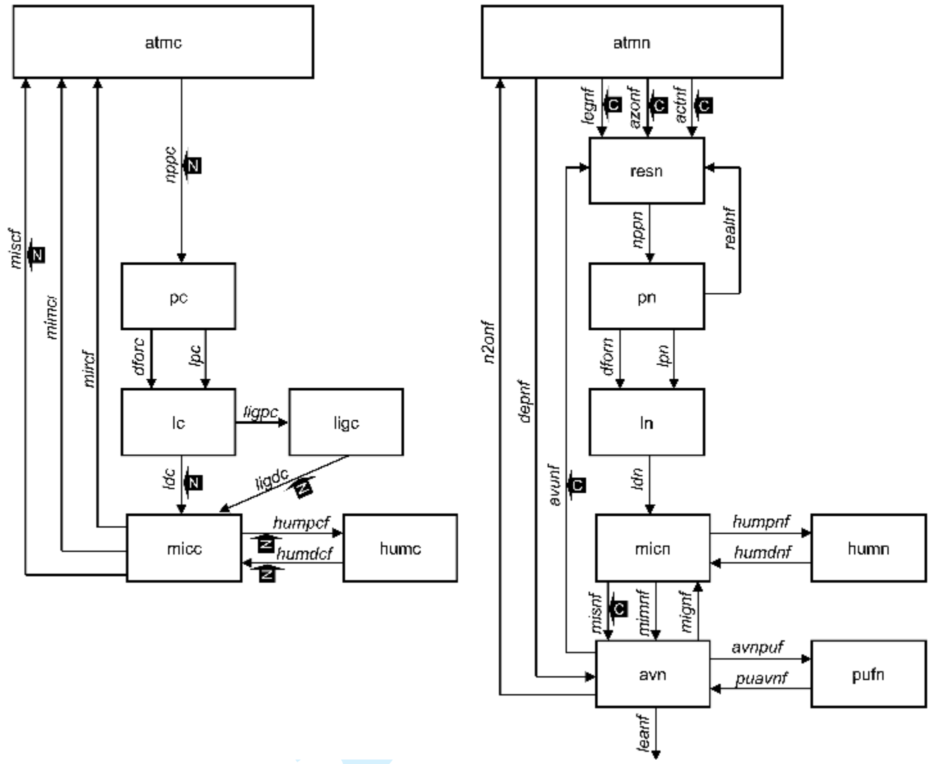

Figure 1: Simplified structure of NCIM's carbon (left) and nitrogen cycles (right) (from Esser 2007). Rectangles denominate pools (state variables), arrows indicate fluxes (processes). The bold black arrows with "C" or "N" indicate the points of direct influences of state variables of one cycle on fluxes of the other. Extensions *c* and *n* in the names of variables refer to the respective cycle. Pools: *atm* atmosphere, *resn* reserve (mobile) nitrogen in plants, *p* phytomass, *l* litter, *lig* lignins (i.e. nitrogen-free components of litter), *mic* soil organisms, *hum* humic substances, *avn* soluble (available) nitrogen compounds in litter and soil, *pufn* adsorbed immobilized nitrogen compounds in soil. *p* and *l* exist fourfold (above and below ground, woody and herbaceous). Fluxes: *npp* net primary productivity (i.e. allocation of C and N compounds in plants), *realnf* re–allocation of N compounds from senescent leaves, *lp* litter production, *defor* deforestation (clearing of vegetation), *ligp* production of nitrogen–free litter components, *ligd* consumption of *lig* by soil organisms, *ld* consumption of litter by soil organisms, *hump* production of humic substances, *humd* consumption of humic substances by soil organisms, *mim* mineralization, *mis* segregation of excess *c* and *n*, *mir* respiration of organisms, *mig* uptake by soil organisms, *avu* uptake by plants, *lea* leaching to groundwater and outfalls, *dep* deposition from anthropogenic sources, *n2o* denitrification to N_2O and N_2, *leg* N_2 fixation by symbionts of legumes, *azo* N_2 fixation by *Azospirillum* symbionts of C4 grasses and cereals, *act* N_2 fixation by actinomycetes and cyanobacteria.

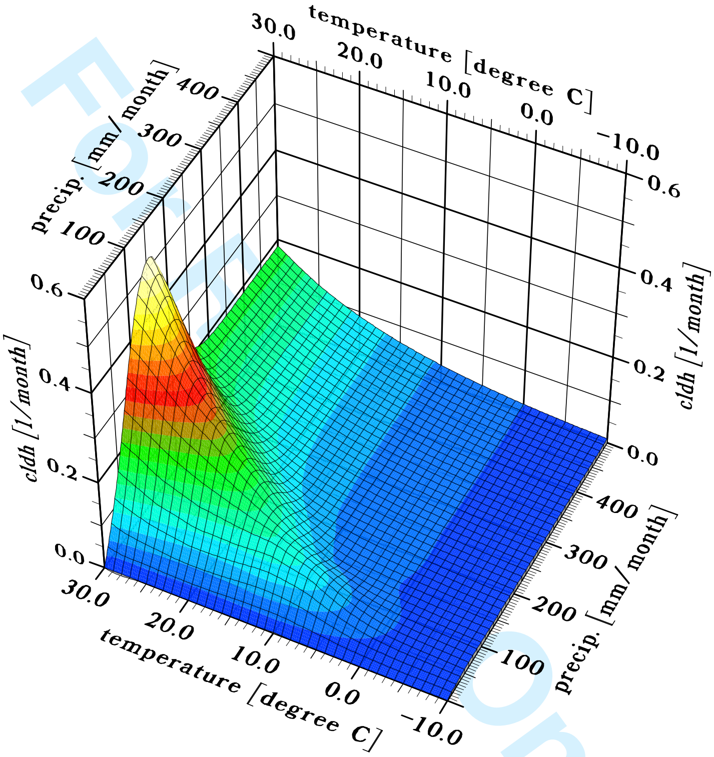

Figure 2: Plot of the coefficient $cldh$ (activity of soil organisms) as a function of monthly precipitation and temperature (equation 13).

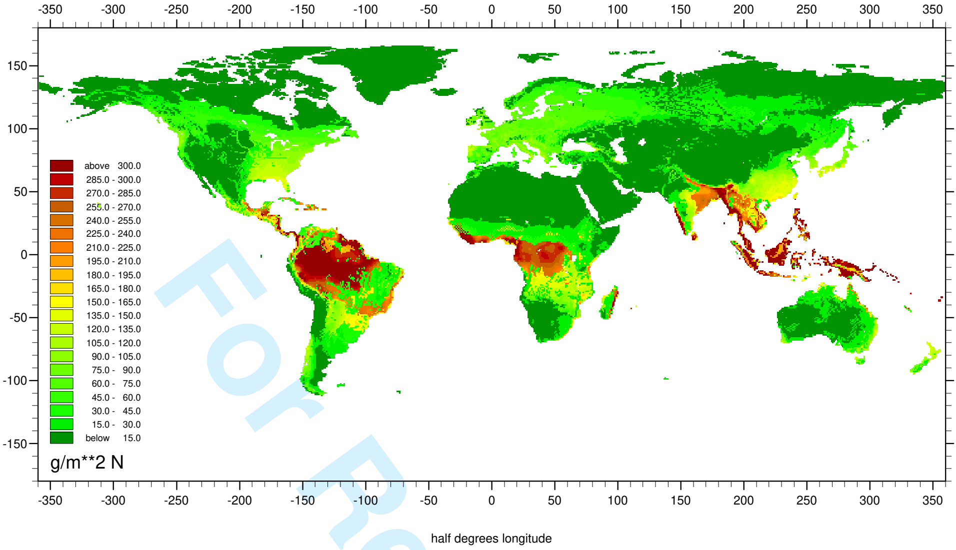

Figure 3: Global modelled distribution of nitrogen [g·m^{-2}] in phytomass for the year 2002 as calculated with NCIM using the configuration of experiment 4 (cn_full) (see table 7).

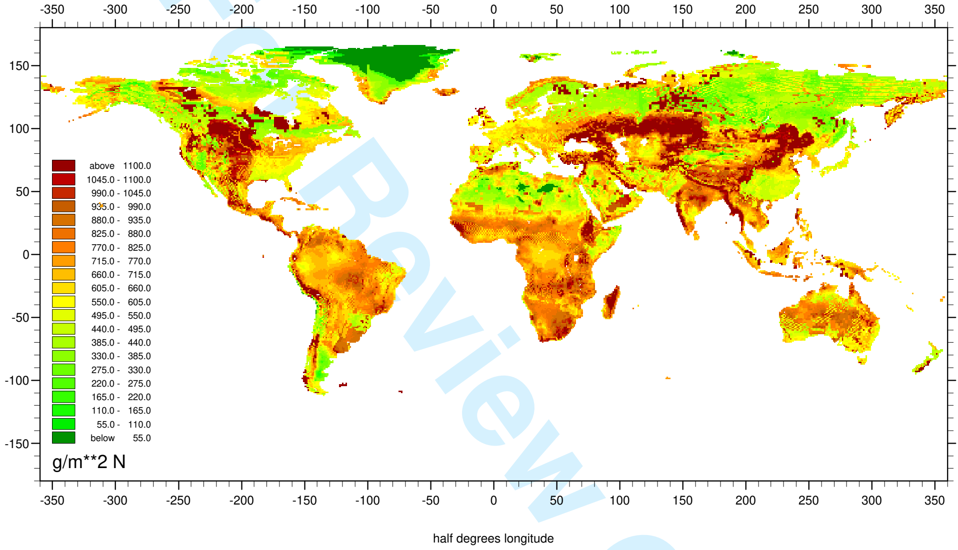

Figure 4: Global modelled distribution of total soil nitrogen [$g \cdot m^{-2}$] for the year 2002 as calculated with NCIM using the configuration of experiment 4 (cn_full) (see table 7).

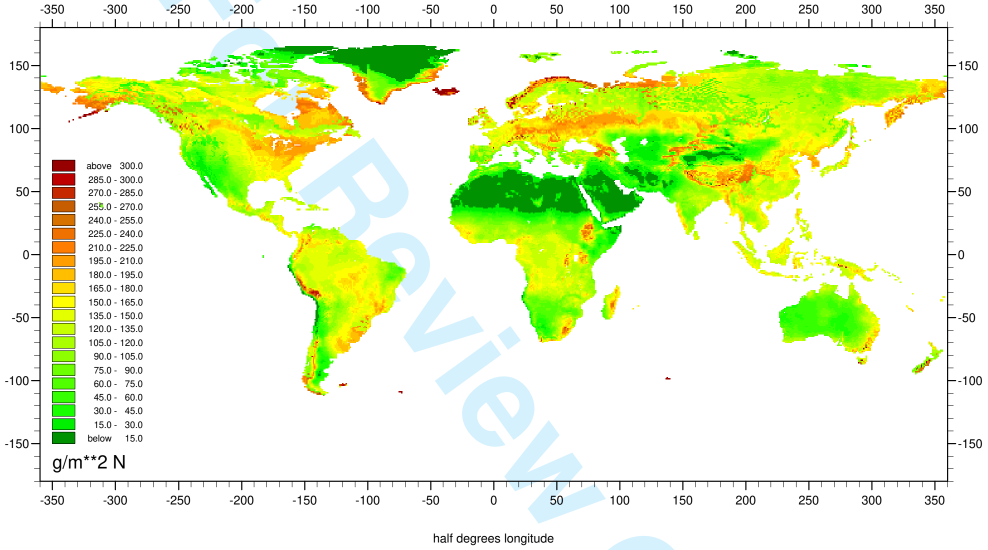

Figure 5: Global modelled distribution of nitrogen [g·m^{-2}] in the biomass of soil organisms for the year 2002 as calculated with NCIM using the configuration of experiment 4 (cn_full) (see table 7).

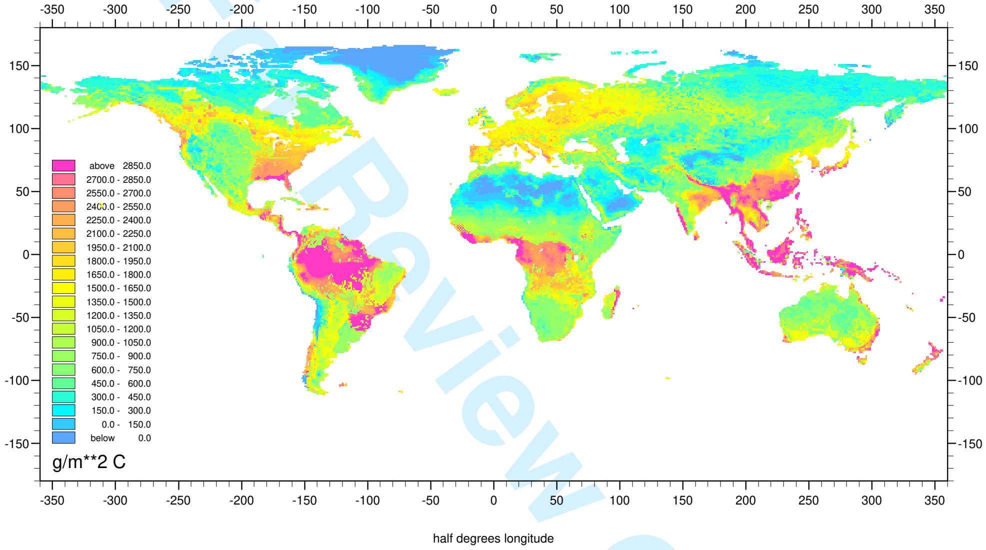

Figure 6: Change of the total biospheric carbon storage from 1860 to 2002 AD [g·m^{-2}] as calculated with NCIM using the configuration of experiment 4 (cn_full) (see table 7).

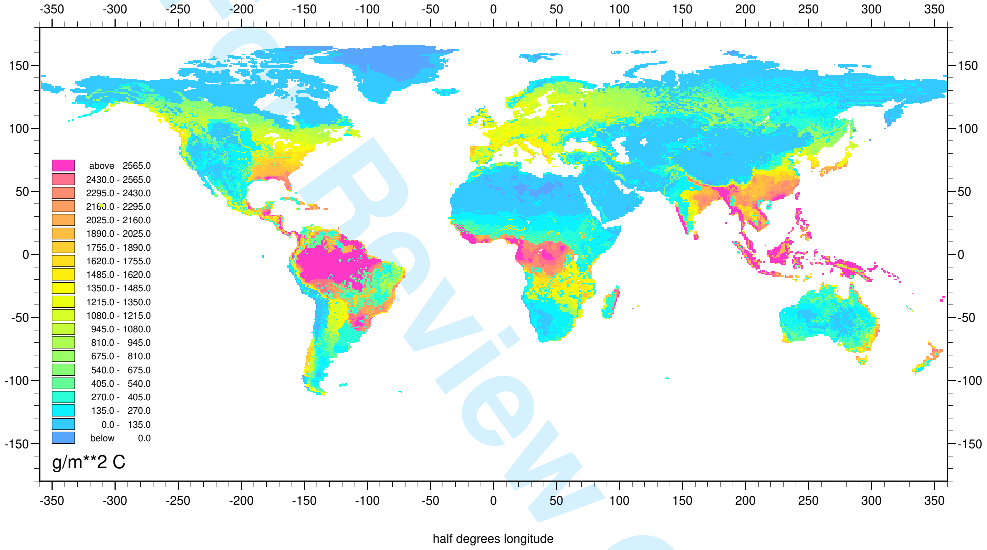

Figure 7: Cange of the carbon storage in the phytomass from 1860 to 2002 AD [g·m^{-2}] as calculated with NCIM using the configuration of experiment 4 (cn_full) (see table 7).

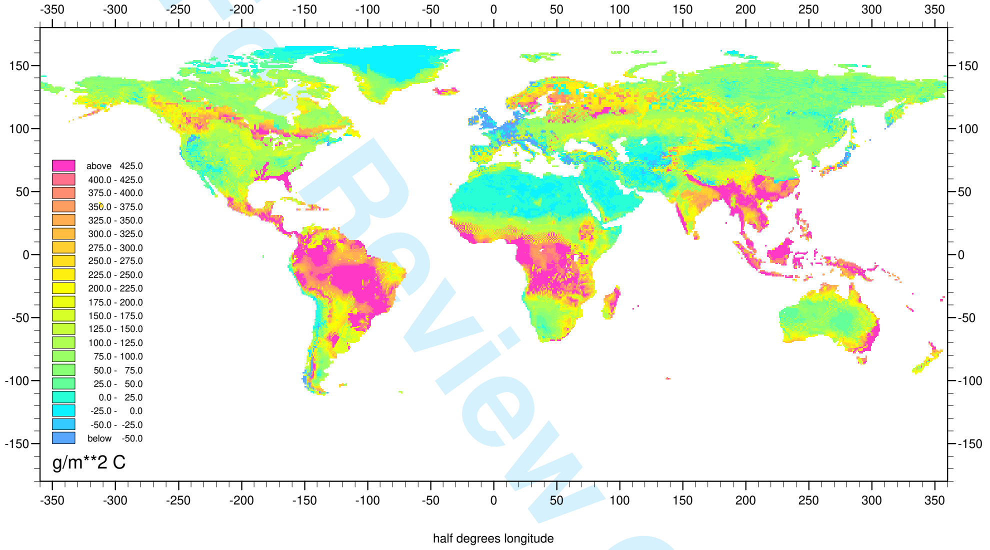

Figure 8: Change of the carbon storage in the biomass of soil organisms from 1860 to 2002 AD [g·m^{-2}] as calculated with NCIM using the configuration of experiment 4 (cn_full) (see table 7).

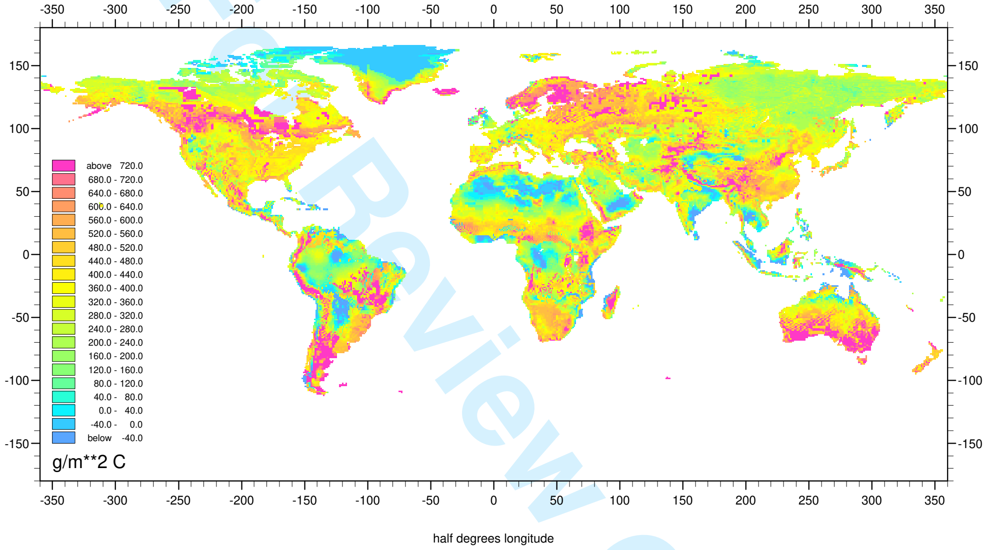

Figure 9: Change of the carbon storage in soil from 1860 to 2002 AD [g·m^{-2}] as calculated with NCIM using the configuration of experiment 4 (cn_full) (see table 7).

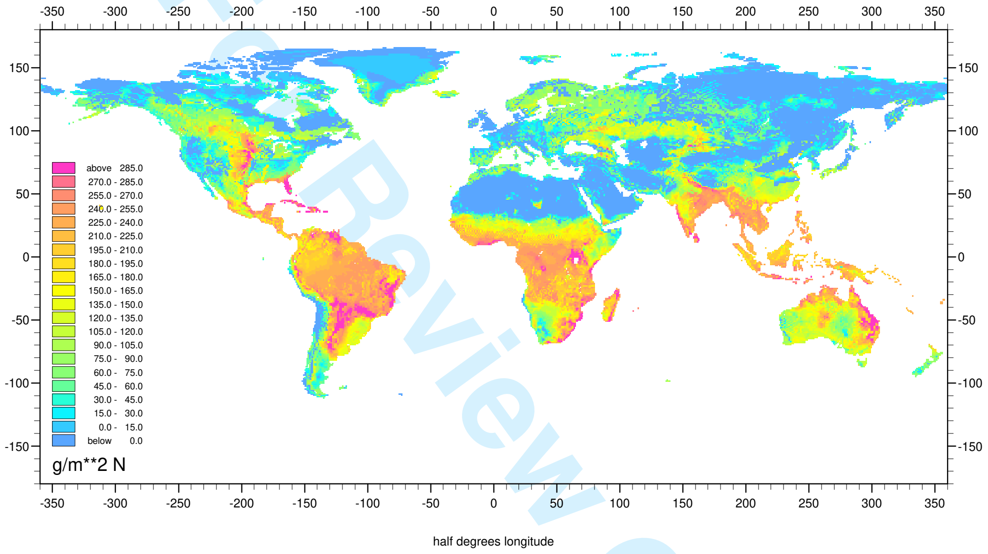

Figure 10: Change of the total biospheric nitrogen storage from 1860 to 2002 AD [g·m^{-2}] as calculated with NCIM using the configuration of experiment 4 (cn_full) (see table 7).