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Carbon-nitrogen feedbacks in the UVic ESCM

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Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Abstract

A representation of the terrestrial nitrogen cycle is introduced into the UVic Earth System Climate Model (UVic ESCM). The UVic ESCM now contains five terrestrial carbon pools and seven terrestrial nitrogen pools: soil, litter, leaves, stem and roots for both elements and ammonium and nitrate in the soil for nitrogen. Nitrogen cycles through plant tissue, litter, soil and the mineral pools before being taken up again by the plant. Biological N_2 fixation and nitrogen deposition represent the external input and loss from the plant-soil system can occur via leaching. Simulated carbon and nitrogen pools and fluxes are in the range of other models and data. Gross primary production (GPP) for the 1990s in the CN-coupled version is $129.6 \text{ Pg C a}^{-1}$ and net C uptake is 0.83 Pg C a^{-1} , whereas the C-only version results in a GPP of $133.1 \text{ Pg C a}^{-1}$ and a net C uptake of 1.57 Pg C a^{-1} . At the end of a transient experiment for the years 1800–2000, where temperature is held constant but CO_2 fertilisation for vegetation is allowed to happen, the CN-coupled version shows an enhanced net C uptake of 1.05 Pg C a^{-1} , whereas in the experiment where CO_2 is held constant and temperature is transient the land turns into a C source of 0.60 Pg C a^{-1} by the 1990s. The arithmetic sum of the temperature and CO_2 effects results in 0.45 Pg C a^{-1} , which is 0.38 Pg C a^{-1} lower than seen in the fully forced model, suggesting a strong non-linearity in the CN-coupled version. Anthropogenic N deposition has a positive effect on Net Ecosystem Production of 0.35 Pg C a^{-1} . Overall, the UVic CN-coupled version shows similar characteristics in terms of C and N pools and fluxes to other CN-coupled Earth System Models.

1 Introduction

There is growing evidence that the availability of nitrogen (N) in terrestrial ecosystems has an important effect on the global carbon (C) cycle (Jain et al., 2009; Gerber et al., 2010; Zaehle et al., 2010b; Bonan and Levis, 2010). The sensitivity of the terrestrial carbon cycle is often expressed as the C sensitivity to CO_2 concentration, β_L in

GMDD

5, 67–118, 2012

CN feedback in the UVic ESCM

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Pg C ppm⁻¹, and the C sensitivity to temperature, γ_L in Pg C K⁻¹ (Friedlingstein et al., 2006; Plattner et al., 2008). The β_L value describes how sensitively the modelled vegetation responds to changes in atmospheric CO₂ concentrations, whereas the γ_L value is mainly determined by the temperature dependent processes, namely photosynthesis, heterotrophic and autotrophic respiration rates.

C-only models estimate β_L to be 1.4 ± 0.5 Pg C ppm⁻¹ and γ_L to be -79 ± 45 Pg C K⁻¹ (Denman et al., 2007). Models that include the interactions between the terrestrial C and N cycle show a decrease in β_L , i.e. a suppressed CO₂ fertilisation effect (Thornton et al., 2009; Sokolov et al., 2008; Bonan and Levis, 2010) and γ_L either becomes less negative or switches from being negative to being positive (Sokolov et al., 2008; Bonan and Levis, 2010), i.e. a smaller release of C from the soil and vegetation pools or even an increase in these pools with increasing temperature. The overall effect of CN interactions on the terrestrial C balance is model dependent and ranges from less C storage to no change in C storage in the future when compared to C-only models (Friedlingstein and Prentice, 2010).

Due to the growing evidence that N potentially has an important impact on the terrestrial C cycle, it is necessary to develop a suite of models that represent the CN interactions. So far, the models range from low resolution models (4° in latitude × 5° in longitude, i.e. Sokolov et al., 2008) to high resolution models (0.5° × 0.5°), i.e. Yang et al. (2009); Jain et al. (2009). The only fully-coupled models in terms of climate-carbon feedbacks so far are that of Sokolov et al. (2008) and Thornton et al. (2009).

With this study, we add another model to this list: we further develop the University of Victoria Earth System Climate Model (UVic ESCM) through the incorporation of the terrestrial CN feedback mechanisms. The UVic ESCM falls in the category of Earth System Models of Intermediate Complexity (EMIC) and is a fully coupled model described in Weaver et al. (2001). In this paper, we describe the N model incorporated into the UVic ESCM, we show the fundamental diagnostics of the N and C cycle and compare the results to existing models or data where appropriate.

**CN feedback in the
UVic ESCM**

R. Wania et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

2 Model description and datasets

Here we use the University of Victoria Earth System Climate Model (UVic ESCM) version 2.9 (Eby et al., 2009). It consists of a primitive equation 3-D ocean general circulation model coupled to a dynamic-thermodynamic sea-ice model and an energy-moisture balance model of the atmosphere with dynamical feedbacks (Weaver et al., 2001). The land surface and terrestrial vegetation components are represented by a simplified version of the Hadley Centre's MOSES land-surface scheme coupled to the dynamic vegetation model TRIFFID (Meissner et al., 2003). Land carbon fluxes are calculated within MOSES and are allocated to vegetation and soil carbon pools (Matthews et al., 2004). Ocean carbon is simulated by means of an OCMIP-type inorganic carbon-cycle model and a NPZD marine ecosystem model (Schmittner et al., 2008). Sediment processes are represented using an oxic-only model of sediment respiration (Archer, 1996).

An earlier version of the UVic-ESCM (version 2.7) has undergone extensive evaluation as part of international model intercomparison projects including the Coupled Carbon Cycle Climate Model Intercomparison Project (Friedlingstein et al., 2006), the Paleoclimate Modelling Intercomparison Project (Weber et al., 2007) and the coordinated thermohaline circulation experiments (Gregory et al., 2005; Stouffer et al., 2006). The model has also been used for multi-century climate projections in support of the IPCC Fourth Assessment Report (Denman et al., 2007; Meehl et al., 2007).

Simulations include the following externally specified forcing: CO₂ and other non-CO₂ greenhouse gases (all applied as reductions in outgoing longwave radiation), stratospheric volcanic aerosols (applied as reductions in incoming shortwave radiation), tropospheric sulphate aerosols (applied as changes in local surface albedo), land use change (also applied as a surface albedo change), and solar variation due to changes in luminosity and the Earth's orbit. Historical land use change maps are used to determine when to change naturally simulated vegetation to agricultural land use. Emissions from land use change are thus internally calculated and would not be

GMDD

5, 67–118, 2012

CN feedback in the UVic ESCM

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



part of any diagnosed (external) anthropogenic carbon emissions for these simulations.

We keep the current structure of MOSES/TRIFFID, the vegetation model within the UVic ESCM generally the same as described in Meissner et al. (2003). This allows us to integrate the model in a C-only mode and in a CN-coupled mode in order to evaluate the differences. The only major change to the model is the addition of a litter C pool as a corresponding C pool for the N litter pool.

2.1 Carbon and nitrogen pools and fluxes

The UVic-CN ESCM has five C pools (leaf, root, wood, litter and soil) and seven N pools (leaf, root, wood, litter, soil, ammonium (NH_4^+) and nitrate (NO_3^-)). The pools and the fluxes between them are shown in Fig. 1 and listed in Table 1. The concept for the N model is adopted from Gerber et al. (2010) with modifications in order to fit the UVic ESCM structure; wherever we use Gerber et al.'s approach, we mention it in the respective section below.

2.1.1 Organic pools

Litterfall for C (C_{LF}) is determined for each plant functional type (PFT) by the size of the carbon pools, C_{leaf} , C_{root} and C_{wood} and by a pool specific turnover rate, η_{root} and η_{wood} (Table 2):

$$C_{\text{LF}} = \sum_{\text{PFT}} \eta_{\text{leaf}} C_{\text{leaf}} + \eta_{\text{root}} C_{\text{root}} + \eta_{\text{wood}} C_{\text{wood}} \quad (1)$$

where $\eta_{\text{leaf}} = \eta_{\text{leaf}}^0 f(T) f(\Theta)$; η_{leaf}^0 is given in Table 2, $f(T)$ and $f(\Theta)$ are given in Eqs. (9) and (10).

Before plants drop their leaves, a fraction of the N is reabsorbed. This is taken account of by the factor r_{leaf} in the calculation of litterfall for N, N_{LF} :

$$N_{\text{LF}} = \sum_{\text{PFT}} \eta_{\text{leaf}} \frac{C_{\text{leaf}}}{\text{CN}_{\text{leaf}}} (1 - r_{\text{leaf}}) + \eta_{\text{root}} \frac{C_{\text{root}}}{\text{CN}_{\text{root}}} + \eta_{\text{wood}} \frac{C_{\text{wood}}}{\text{CN}_{\text{wood}}} \quad (2)$$

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



where CN_{leaf} , CN_{root} and CN_{wood} are the C/N ratios of leaves, roots and wood (see Sect. 2.4.1). The C/N ratio of litterfall is different than that of the plant source because a portion of leaf nitrogen (r_{leaf}) is reabsorbed by the plant before abscission.

Litterfall (C_{LF} , N_{LF}) is added to the litter pools (C_{L} , N_{L}), whereas humification (C_{HUM} , N_{HUM}) and litter respiration (C_{RESPL}) and mineralisation (N_{MINL}) are subtracted from the litter pools:

$$\frac{dC_{\text{L}}}{dt} = C_{\text{LF}} - C_{\text{HUM}} - C_{\text{RESPL}} \quad (3)$$

$$\frac{dN_{\text{L}}}{dt} = N_{\text{LF}} - N_{\text{HUM}} - N_{\text{MINL}} \quad (4)$$

Humification is the transfer of organic material from the litter to the soil pool (Eqs. 5 and 6), litter respiration is the decomposition of organic C in litter to form CO_2 (Eq. 7) and litter mineralisation is the decomposition of organic N in litter to form ammonium (NH_4^+) (Eq. 8):

$$C_{\text{HUM}} = f(T)f(\Theta)k_{\text{L}}C_{\text{L}}(1 + \xi[N_{\text{min,av}}])\tau \quad (5)$$

$$N_{\text{HUM}} = f(T)f(\Theta)k_{\text{L}}N_{\text{L}}(1 + \xi[N_{\text{min,av}}])\tau \quad (6)$$

$$C_{\text{RESPL}} = f(T)f(\Theta)k_{\text{L}}C_{\text{L}}(1 + \xi[N_{\text{min,av}}])(1 - \tau) \quad (7)$$

$$N_{\text{MINL}} = f(T)f(\Theta)k_{\text{L}}N_{\text{L}}(1 + \xi[N_{\text{min,av}}])(1 - \tau) \quad (8)$$

where the temperature dependence $f(T)$ is a function of soil temperature (Cox, 2001, Eq. 17):

$$f(T) = q_{10}^{0.1(T_s - 25)} \quad (9)$$

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



where $q_{10} = 2.0$ and T_s is the soil temperature in °C and $f(\Theta)$ is a function of soil moisture (Cox, 2001, Eq. 18)

$$f(\Theta) = \begin{cases} 1 - 0.8(S - S_0) & \text{for } S > S_0 \\ 0.2 + 0.5 \left(\frac{S - S_w}{S_0 - S_w} \right) & \text{for } S_w < S \leq S_0 \\ 0.2 & \text{for } S \leq S_w \end{cases} \quad (10)$$

where S , S_w and S_0 are the soil moisture, the wilting point soil moisture and the optimum soil moisture (Cox, 2001, Eqs. 19–21). Other terms used in Eqs. (5) and (8) are a specific litter turnover rate k_L (Table 3), the litter pool size (C_L , N_L) and the concentration of available, mineral N, [$N_{\min,av}$] (see Table 4 for relationships between various mineral N pools and concentrations). The parameter ξ (Table 3) describes the dependence of respiration and mineralisation on available mineral nitrogen concentration and is taken from Gerber et al. (2010). The fraction τ (Table 3) defines how much of the litter is humified and transferred to the soil pool and how much is decomposed (C_{RESPL} , N_{MINL}).

Humified litter material is transferred to the soil pools, C_s and N_s , which are decreased by respiration (C_{RESPS}) in case of C (Eq. 11) and by mineralisation (N_{MINS}) in case of N (Eq. 12). The organic N soil pool, N_s , is further increased by the immobilisation of ammonium and nitrate (NH_4^{IMM} , NO_3^{IMM}) (Eq. 12).

$$\frac{dC_s}{dt} = C_{HUM} - C_{RESPS} \quad (11)$$

$$\frac{dN_s}{dt} = N_{HUM} - N_{MINS} + NH_4^{IMM} + NO_3^{IMM} \quad (12)$$

where soil respiration, C_{RESPS} ,

$$C_{RESPS} = f(T)f(\Theta)k_S C_s \quad (13)$$

and soil mineralisation, N_{MINS} ,

$$N_{MINS} = f(T)f(\Theta)k_S N_s \quad (14)$$

CN feedback in the UVic ESCM

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



depend on the temperature function (Eq. 9) and moisture function (Eq. 10) mentioned above, a specific turnover rate k_S (Table 3) and the size of the pool (C_S , N_S). The addition of the immobilisation terms to the soil N pool, (N_S), ensures a stable soil C/N ratio, and balances out any deficit of N which may arise when the incoming material via humification has a high C/N ratio.

2.1.2 Mineral pools

The UVic-CN model has two separate N mineral pools, ammonium (NH_4^+) and nitrate (NO_3^-); for simplicity, the pools are labelled NH_4 and NO_3 hereafter. The rates of change of these two pools are given by:

$$\frac{d\text{NH}_4}{dt} = N_{\text{MINL}} + N_{\text{MINS}} + \text{BNF} + \text{NH}_4^{\text{DEP}} - \text{NH}_4^{\text{UP}} - \text{NH}_4^{\text{LEA}} - \text{NH}_4^{\text{IMM}} - \text{NIT} \quad (15)$$

and

$$\frac{d\text{NO}_3}{dt} = \text{NIT} + \text{NO}_3^{\text{DEP}} - \text{NO}_3^{\text{UP}} - \text{NO}_3^{\text{LEA}} - \text{NO}_3^{\text{IMM}}. \quad (16)$$

Mineralisation of N from litter (N_{MINL}) and soil pools (N_{MINS}) are the autochthonous (i.e. from within the ecosystem) inputs into the NH_4 pool, whereas biological nitrogen fixation (BNF; Sect. 2.2) and deposition of NH_4^+ (NH_4^{DEP} ; Sect. 2.2) are the allochthonous (i.e. from outside the ecosystem) input variables. Ammonium may be taken up by the plant (NH_4^{UP}), lost by leaching (NH_4^{LEA}), immobilised by microorganisms (NH_4^{IMM}) or turned into NO_3^- (nitrification, NIT). Nitrification (NIT) represents the only autochthonous flux for NO_3^- , the only other input being the allochthonous input of atmospheric deposition of NO_3^- (NO_3^{DEP}). Nitrate may be taken up by plants (NO_3^{UP}), leached from the soil (NO_3^{LEA}) or immobilised by microorganisms (NO_3^{IMM}). Equations (15) and (16) follow Gerber et al. (2010) with the modification that BNF is added to the NH_4 pool, rather than being put directly into a vegetation N pool.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The calculation of plant uptake, NH_4^{UP} and NO_3^{UP} ($\text{kg N m}^{-2} \text{a}^{-1}$), is based on Gerber et al. (2010) and is separated into active (first part on RHS in Eqs. (17) and (18)) and a passive uptake (second part on RHS in Eqs. (17) and (18)). The active plant uptake represents the part of the uptake that is driven by exchange of ions between the roots and the soil, i.e. for each NH_4^+ molecule taken up, a proton is exuded, whereas the passive uptake transports the N contained in the soil water via the transpirational water stream.

$$\text{NH}_4^{\text{UP}} = \sum_{\text{PFT}} \left(\frac{v_{\text{max}} C_{\text{root}} \text{NH}_{4(\text{av})}}{h_{\text{S}}(k_{\rho,1/2} + [\text{N}_{\text{min}(\text{av})}])} + [\text{NH}_{4(\text{av})}] Q_{\text{T}} \right) \quad (17)$$

$$\text{NO}_3^{\text{UP}} = \sum_{\text{PFT}} \left(\frac{v_{\text{max}} C_{\text{root}} \text{NO}_{3(\text{av})}}{h_{\text{S}}(k_{\rho,1/2} + [\text{N}_{\text{min}(\text{av})}])} + [\text{NO}_{3(\text{av})}] Q_{\text{T}} \right) \quad (18)$$

Active plant uptake depends on the PFT-dependent maximum uptake rate v_{max} per unit root mass ($\text{kg N}(\text{kg root C})^{-1} \text{a}^{-1}$), C_{root} (kg C m^{-2}), soil depth h_{S} (m), the half-saturation constant $k_{\rho,1/2}$ (kg N m^{-3}) (see Tables 3 and 2 for values), the available ammonium $\text{NH}_{4(\text{av})}$ (kg N m^{-2}) and the total concentration of available mineral N, $[\text{N}_{\text{min}(\text{av})}]$ (kg N m^{-3}) (Table 4 lists the relationships between different mineral N pools).

The second part on RHS in Eqs. (17) and (18) expresses the passive plant uptake in form of the PFT-dependent transpiration rate Q_{T} (m s^{-1}) and the available NH_4^+ $[\text{NH}_{4(\text{av})}]$ or NO_3^- $[\text{NO}_{3(\text{av})}]$ concentration (kg N m^{-3}). We impose lower and upper boundaries for the plant uptake: the minimum plant uptake rate is set to a value to meet the minimum N requirements of each PFT and the maximum plant uptake rate is set so that no excess N is stored in the plants. The minimum N requirement is based on the current C contents in leaf, root and wood and the maximum C/N ratios, whereas for the maximum N requirement, we use the minimum C/N ratios. Details on how the boundaries are imposed are given in Sect. 2.4.1.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The immobilisation of NH_4^+ and NO_3^- (NH_4^{IMM} , NO_3^{IMM}) via microorganisms occurs when the soil quality decreases, i.e. soil C/N ratio (CN_{soil}) increases; in the UVic-CN immobilisation happens when soil C/N is greater than 13 – a value in the range used by Gerber et al. (2010) and Zaehle and Friend (2010); consequently, the soil C/N ratios in the UVic CN model are kept more or less constant. Relating immobilisation rates to the C/N ratio is controversial as biomass and metabolic state of microorganisms seem to be better predictors of immobilisation rates (Bengtsson et al., 2003) than soil C/N ratios. However, microbial biomass and their metabolic state are not variables that are ready to be included into a global Earth System Model. Further, we do not know if soil C/N ratios will not change under CO_2 fertilisation and higher N demands. The concept of the equations for immobilisation is taken and adjusted from Gerber et al. (2010):

$$\text{NH}_4^{\text{IMM}} = f(T)f(\Theta)k_L(1 + \xi N_{\text{min(av)}})\tau \frac{\text{NH}_{4(\text{av})}}{N_{\text{min(av)}}} \frac{C_L}{\text{CN}_{\text{soil}}} \quad (19)$$

$$\text{NO}_3^{\text{IMM}} = f(T)f(\Theta)k_L(1 + \xi N_{\text{min(av)}})\tau \frac{\text{NO}_{3(\text{av})}}{N_{\text{min(av)}}} \frac{C_L}{\text{CN}_{\text{soil}}} \quad (20)$$

where NH_4^{IMM} and NO_3^{IMM} are in ($\text{kg N m}^{-2} \text{a}^{-1}$), the temperature $f(T)$ and moisture function $f(\Theta)$ are given in Eqs. (9) and (10), k_L is the specific litter turnover rate (a^{-1} , Table 3), ξ is a modifier of the N dependent litter decomposition rate ($\text{m}^3 \text{kg N}^{-1}$, Table 3), $N_{\text{min(av)}}$, $\text{NH}_{4(\text{av})}$ and $\text{NO}_{3(\text{av})}$ are the total, NH_4^+ and NO_3^- available mineral N pools (kg N m^{-2} , Table 4), τ is the fraction of decomposition transferred to the soil pool (Table 3), C_L is the litter C pool (kg C m^{-2}) and CN_{soil} is the C/N ratio of the soil (kg C (kg N)^{-1}).

Nitrification (NIT) in $\text{kg N m}^{-2} \text{a}^{-1}$ follows the same concept as in Gerber et al. (2010):

$$\text{NIT} = f(T)f(\Theta)k_{\text{Nit}}\text{NH}_{4(\text{av})} \quad (21)$$

CN feedback in the UVic ESCM

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



but uses the UVic ESCM inherent temperature $f(T)$ (Eq. 9) and moisture function $f(\Theta)$ (Eq. 10), a maximum nitrification rate, k_{Nit} (a^{-1} , Table 3) and the available NH_4^+ pool, $\text{NH}_{4(\text{av})}$ (kg N m^{-2} , Table 4).

2.2 Nitrogen input

5 External nitrogen inputs consist of biological nitrogen fixation (BNF) and atmospheric deposition of NH_4^+ (NH_4^{DEP}) and NO_3^- (NO_3^{DEP}).

During the spin-up period, we use the relationship between BNF and evapotranspiration (ET) based on Cleveland et al. (1999) that has been used in CN models of Zaehle and Friend (2010) and Yang et al. (2009):

$$10 \text{ BNF} = 0.1(0.0234 \text{ ET} - 0.172)/1000 \quad (22)$$

where the original units are modified to $\text{kg N m}^{-2} \text{ a}^{-1}$ for BNF and mm a^{-1} for ET. However, using this approach for transient simulations (1800–1999) in the UVic ESCM leads to a significant reduction in NPP at the end of the 20th century due to a reduction of ET with increasing CO_2 concentrations and we therefore opt for the apparently more robust relationship used by the Community Climate Model CLM4 (Thornton et al., 2009) and relate total annual BNF to NPP. After the UVic-CN model has come to equilibrium for the year 1800 using the relationship between evapotranspiration (ET) and BNF following Eq. (22) we obtain a relationship, ϵ , between BNF and net primary production (NPP):

$$20 \text{ BNF} = \epsilon \text{ NPP} \quad (23)$$

where NPP is in $\text{kg C m}^{-2} \text{ a}^{-1}$ and ϵ is $2.73 \text{ g N (kg C)}^{-1}$ and gives 180 Tg N a^{-1} for an NPP of 66 Pg N a^{-1} .

25 Nitrogen deposition takes place in dry and wet form of NH_x (NH_4^{DEP}) and NO_y (NO_3^{DEP}) and occurs close to the source of pollution. Nitrogen deposition onto terrestrial ecosystems has increased by a factor of 3.6 since the pre-industrial period and

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



is projected to double again between 1990 and 2050 (Galloway et al., 2004). The main centres of deposition in the early 1990's are the Eastern United States, Central Europe, India, Southeast Asia and Southeastern Brazil, which are likely to intensify and spread in the future (Galloway et al., 2004). Here, we use the global annual, natural and anthropogenic, deposition rates of NH_x and NO_y by Dentener (2006) for the time slices of 1860, 1993 and 2050, which are regridded from the original $5^\circ \times 3.75^\circ$ map to UVic ESCM's resolution of $3.6^\circ \times 1.8^\circ$ and interpolated between time slices in order to obtain annual deposition rates for the years 1860–1999; deposition rates of the year 1860 are used for the period 1800–1859.

2.3 Nitrogen loss

Mineral N in the UVic ESCM can be lost from the soil via leaching:

$$\text{NH}_4^{\text{LEA}} = Q_{\text{D}}[\text{NH}_{4(\text{av})}] \quad (24)$$

$$\text{NO}_3^{\text{LEA}} = Q_{\text{D}}[\text{NO}_{3(\text{av})}] \quad (25)$$

and is related to the runoff Q_{D} (m a^{-1}) and the concentration of available NH_4^+ and NO_3^- (kg N m^{-3}). The available N depends on the sorption factor b_{NH_4} and b_{NO_3} (Table 3) and makes NH_4^+ less available for leaching than NO_3^- due to the cation binding capacity of soils. Gaseous losses of N are not considered in the current version.

2.4 Vegetation nitrogen

2.4.1 Allocation of N to plant organs

Nitrogen is allocated to leaves, roots and wood: the allocation of N to wood follows a fixed C/N ratio of $330 \text{ kg C (kg N)}^{-1}$ for broad-leaved and needle-leaved trees and for shrubs (Sitch et al., 2003). While the C/N ratio of wood is fixed, the C/N ratios of leaves

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



and roots vary between a minimum and maximum value (Table 2). The change in total vegetation N (N_V) is estimated by:

$$\frac{dN_V}{dt} = \text{NH}_4^{\text{UP}} + \text{NO}_3^{\text{UP}} - N_{\text{LF}} \quad (26)$$

where NH_4^{UP} and NO_3^{UP} are the N that the plant takes up in form of NH_4^+ and NO_3^- (Eqs. 17 and 18) and N_{LF} is the N lost via litterfall (Eq. 2). Vegetation N (N_V) is spread over the three plant N pools by first allocating N to wood following the fixed C/N ratio, then allocating a minimum amount of N to roots to meet the maximum C/N ratio and then adding the remaining N to the leaf N pool. If there is more N available than needed to fill up the N_{leaf} pool and $\text{CN}_{\text{Leaf}} < \text{CN}_{\text{Leaf,min}}$ then we set $\text{CN}_{\text{Leaf}} = \text{CN}_{\text{Leaf,min}}$ and any excess N is added to the roots. In that way, the N requirements for leaves are met before the ones for roots and only if there is sufficient N available, root N levels increase. If $\text{CN}_{\text{Root}} < \text{CN}_{\text{Root,min}}$ then we set $\text{CN}_{\text{Root}} = \text{CN}_{\text{Root,min}}$ and any excess N is added back to the NO_3^- pool and subtracted from the uptake. If both, CN_{Leaf} and CN_{Root} are at their minimum level, the plant N status is optimal for plant growth. The reason for choosing this setup is to allow flexible root and leaf C/N ratios in order to avoid immediate N deficiency stress when enhancing C acquisition rates. It has been shown that root C/N ratios (Pendall et al., 2004; Gai-ping et al., 2006) as well as leaf C/N ratios (Liu et al., 2005) can increase in Free Air CO_2 Experiments experiments (FACE), though the interdependence between changes in root and leaf C/N ratios still needs investigation.

Under N limitation in the model, i.e., there is not enough N available to meet the requirements $\text{CN}_{\text{Leaf}} > \text{CN}_{\text{Leaf,max}}$, then, first, leaching is reduced by up to 100 % and if more N is needed, then immobilisation is reduced by up to 50 % and added to the plant uptake. In both cases, the NO_3^- fluxes are adjusted before the NH_4^+ ones. Reducing leaching and immobilisation in favour of increasing uptake gives plants in the model preferential access to mineral nitrogen pools. If thereafter the N uptake still does not meet the N demand, extra N is taken directly from the NO_3^- or NH_4^+ at the same proportions as uptake happens and is added to the leaf N pool. This setup ensures that,

CN feedback in the UVic ESCM

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



given the current C stocks in the plant biomass, the minimal requirement for N to fulfil the C/N ratios are always met.

2.4.2 N effect on photosynthesis

One of the determining factors in the rate of photosynthesis is the activity of the enzyme Rubisco, which correlates well with leaf N concentration (e.g., Evans, 1983). This relationship is reflected in the UVic ESCM by linking the maximum rate of carboxylation by Rubisco, $V_{c,max}$ ($\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) to leaf N, or in this case to the inverse of the leaf C/N ratio.

$$V_{c,max} = \lambda \frac{1}{\text{CN}_{\text{leaf}}} \quad (27)$$

We substitute the top canopy leaf N concentration (n_1) in the original equation (Cox et al., 1999, Eq. 21), which is fixed for each PFT, by the inverse of the calculated average canopy leaf C/N ratio (CN_{leaf}). The constant of proportionality λ is 0.004 for C_3 and 0.008 for C_4 PFTs (Cox et al., 1999). Equation (27) means that photosynthetic activity and therefore plant productivity is reduced when CN_{Leaf} increases, but in the model it never goes towards zero because of N limitation as CN_{Leaf} has a maximum value (Table 2). We opt for using the average canopy leaf C/N ratio rather than top leaf C/N ratio as done in Cox et al. (1999) as there is evidence that it is not the C/N ratio of leaves that varies within a canopy, but the leaf mass area per unit area and with it the N mass per unit area (Hollinger, 1996). Hence, as long as N concentration is expressed in kg N (kg C)^{-1} , i.e. as inverse of the C/N ratio, as done in the UVic model, we can assume that there is no need for varying C/N ratios of leaves within the canopy (Thornton and Zimmermann, 2007).

2.5 Model simulations

The model is integrated either with CN feedbacks switched on (UVic CN-coupled mode) or with both, the vegetation and soil CN feedbacks, switched off (UVic C-only mode).

CN feedback in the UVic ESCM

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



To switch off the soil CN feedbacks, the term $(1 + \xi[N_{\min,av}])$ is omitted from Eqs. (5) to (8) and to turn off the vegetation CN feedback, the leaf N concentrations (n_l) given as inverse ($1/n_l$) in Table 2 are used in Eq. (27) instead of the calculated leaf C/N ratios (CN_{leaf}). Values for n_l in the UVic C-only mode are set so that a comparable GPP between the C-only and the CN-coupled mode is achieved.

Both model versions are spun-up until the soil C pool changed less than 0.5 % per century. The models are then integrated transiently from 1800 to 1999 in either the CN-coupled mode or the C-only mode. We use the usual set of forcing for the UVic ESCM (orbital parameters, solar constant, volcanic activity, sulphate concentrations, land ice cover, atmospheric CO_2 concentrations, non- CO_2 greenhouse gas concentrations and land use change), the only new forcing for the UVic-CN version is the nitrogen deposition derived as described in Sect. 2.2. Nitrogen deposition affects the C cycle in the model only when the CN feedbacks are switched on.

Five experiments are conducted, three with the CN-coupled version (E1–E3), two with the C-only version (E4–E5). The experiments are listed in Table 5 and are similar to other studies that used radiatively coupled/uncoupled runs (e.g., Zaehle et al., 2010b). The runs are transient runs for the time period 1800 to 1999.

A fully forced simulation is conducted for the CN-coupled version (FF1) and the C-only version (FF2), in which all of the relevant forcings are used. The experiments also included radiatively coupled simulations, where the climate experiences the radiative effect of increasing atmospheric CO_2 concentrations, but the vegetation experiences no CO_2 fertilisation effect due to atmospheric CO_2 concentrations being held constant at the 1800 level (E1 and E4) and radiatively uncoupled simulations, where the climate sees a constant CO_2 concentration at 1800 levels, but the vegetation experiences the transient CO_2 concentrations (E2 and E5). The third experiment for the CN-coupled version held N deposition constant at 1800 levels, whereas in E1 and E2 they are transient.

**CN feedback in the
UVic ESCM**

R. Wania et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

Sensitivities of the terrestrial C pool to CO₂ concentration (β_L) and air temperature (γ_L) are calculated following Bonan and Levis (2010, Eqs. 2a and 3a):

$$\beta_L = \frac{\Delta C_L^{(FF-Climate)} - \Delta C_L^{FF}}{\Delta C_A} \quad (28)$$

and

$$\gamma_L = \frac{\Delta C_L^{(FF-Vegetation)} - \Delta C_L^{FF}}{\Delta T_L} \quad (29)$$

where ΔC_L^{FF} , $\Delta C_L^{(FF-Climate)}$ and $\Delta C_L^{(FF-Vegetation)}$ are changes in land C in the different experiments (Table 5), ΔC_A is the change of atmospheric CO₂ concentration and ΔT_L the change in 2 m land surface temperature between the period 1800–1804 and the period 1995–1999.

3 Results and discussion

3.1 Nitrogen pools

The spatial distribution of N stocks in vegetation (Fig. 2a) shows a similar pattern to C stocks (Fig. 7a) with highest N content of 30–50 g N m⁻² in forest areas. Most tropical forests fall in the 30–40 g N m⁻² range, with lower values in some parts of the Amazon. The boreal zones in North America and Europe show with 30–40 g N m⁻² higher N contents than in boreal Russia. Simulated vegetation N stocks are lower compared to Gerber et al. (2010) and much lower than Xu-Ri and Prentice (2008) and Yang et al. (2009). The latter two studies simulated plant N contents of 150 to 400 g N m⁻² in tropical forests, which results in vegetation CN ratios of 37.5 to 133 assuming a vegetation C stock in tropical forests of 15–20 kg C m⁻² (e.g., Sitch et al., 2003). The vegetation CN ratios obtained by the UVic CN-coupled model are shown in Fig. 3 and are between 250 and 300 in tropical forests. The dominant factor for the overall CN ratio of

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



CN feedback in the UVic ESCM

R. Wania et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



the vegetation is the wood CN ratio as wood contributes between 70–94 % of tropical plant biomass (Vitousek et al., 1988; Malhi et al., 1999). Observed wood CN ratios for tropical trees vary from 95 to 730 (Martius, 1992) and any modelled vegetation N content will strongly depend on the value chosen for the PFT-dependent wood CN ratios.

5 The global vegetation N pool in the UVic model is 2.94 Pg N close to the estimate of Zaehle et al. (2010b) (Table 6), but much lower than the estimates of Lin et al. (2000) (16 Pg N) and Yang et al. (2009) (18 Pg N). However, given that the current estimate of vegetation C is between 560 and 652 Pg C (Saugier and Roy, 2001), a vegetation N pool of 16–18 Pg N would result in an – in our opinion – unreasonably low average
10 global vegetation CN ratio of 31–41, whereas a vegetation N pool of 2.94 Pg N as found in this study results in a global vegetation CN ratio of 190–222, values closer to what we expect from the fact that vegetation biomass is dominated by wood biomass with a high C/N ratio.

The sum of the simulated soil and litter N stocks are 0–2 kg N m⁻² (Fig. 2b) and therefore lower than the N values shown in the IGBP-DIS database (Fig. 2c). Since soil N content in the model is tied to soil C content via a fixed CN ratio, lower C stocks in the UVic-CN model (Fig. 7) lead to lower N stocks compared to the IGBP-DIS data (frequently over 30 kg C in the boreal zone) (Global Soil Data Task Group, 2000). The lack of permafrost and peatlands in the UVic-CN model is the likely reason for the underestimation of boreal C stocks (Wania et al., 2009). The global soil N stocks in the UVic-CN model are 113 Pg N. This compares well to Zaehle et al. (2010b) (100 Pg N),
20 to Yang et al. (2009) (65 Pg N in for the top 30 cm of soil) and the information from soil data bases by Post et al. (1985); Batjes (1996) (95–140 Pg N).

In general, tropical forests show the highest simulated vegetation C/N ratios (Fig. 3a),
25 with some extra-tropical exceptions such as in Chile, Mexico and South Africa where both tree PFTs occur. C/N ratios in temperate forests in North America are between 200 and 250 and decrease northwards to 150–200 kg C (kg N)⁻¹, a value range also seen for the Eurasian boreal zone. Litter C/N ratios follow the vegetation C/N ratio closely (Fig. 3b) and correspond well to observed values (White et al., 2000), who

reported litter C/N ratios of 55 for deciduous broadleaved forests, 93 for evergreen needleleaved forests, 45 for grass and 75 for shrubs. Both the modelled litter and vegetation C/N ratios are lower in areas where the percentage of leaf and root biomass is higher. In boreal areas simulated leaves and roots constitute about 10% of total biomass, whereas in some tropical regions leaves and roots constitute only 3% of the total biomass compared to observed 4.5% in northern conifer ecosystems and 1.9% in tropical closed forests (Vitousek et al., 1988). The difference in the percentage of leaves and roots explains the higher C/N ratios in vegetation and litter in the tropics.

In the absence of reliable observation based estimates of NO_3^- in desert areas, the evaluation of simulated N pools from any model remains difficult. Ammonium and nitrate pools (Fig. 4) show some similarity to the results shown in Xu-Ri and Prentice (2008, Figs. 12 and 13). Both Xu-Ri and Prentice (2008) and the UVic-CN simulate higher NH_4^+ in colder regions and higher NO_3^- in desert areas. High NO_3^- concentrations have been observed in sub-soils of some deserts (Walvoord et al., 2003) and the reason for the high concentrations of NO_3^- in desert areas in the UVic-CN model is the small but constant input of atmospheric NO_3^- which accumulates over time due to limited output such as vegetation uptake and leaching. The higher NH_4^+ concentrations in colder regions can be explained by lower leaching and nitrification rates. The global soil NO_3^- and NH_4^+ pools are simulated to be 14.8 Pg N and 1.2 Pg N, respectively, which is higher than Xu-Ri and Prentice (2008)'s estimates of 0.58 Pg N and 0.36 Pg N for NO_3^- and NH_4^+ , however it is lower than the 25 Pg N of total mineral N estimated by Lin et al. (2000). Without the knowledge of how much NO_3^- is stored in desert areas, it will remain difficult to evaluate the simulated mineral N pools in any model.

3.2 Nitrogen fluxes

Global annual rates of plant N uptake ($873.2 \text{ Tg N a}^{-1}$) are lower than estimates from other models (1002 to 1126 Tg N a^{-1}) (Xu-Ri and Prentice, 2008; Yang et al., 2009; Zaehle et al., 2010b). As discussed above, the vegetation CN ratios in the UVic-CN

CN feedback in the UVic ESCM

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



model are higher compared to other models, which reduces the demand for plant N uptake and explains the lower uptake rates. Generally, uptake rates in the UVic-CN model range from 3–9 g N m⁻² a⁻¹ in temperate and boreal regions to 3–15 g N m⁻² a⁻¹ in tropical regions (Fig. 5a). Higher values of 15–23 g N m⁻² a⁻¹ can be found in tropical grasslands (in this case in sub-Saharan Africa, India, Southern Brazil and Northern Australia). Nitrogen uptake rates in the ORCHIDEE-CN model are estimated to be 4, 8 and 13 g N m⁻² a⁻¹ in boreal, temperate broadleaved and tropical regions respectively with maximal uptake rates of 30 g N m⁻² a⁻¹ found in grasslands (Zaehle et al., 2010b).

The spatial distribution of leaching is similar to that of runoff with highest values in the tropics and negligible in drier and colder regions (Fig. 5b). Global annual N losses via leaching sum up to 222 Tg N a⁻¹. Due to the lack of gaseous N losses in the UVic ESCM, the model's leaching flux needs to be compared to the sum of leaching and gaseous fluxes in other models. Zaehle et al. (2010b) estimate total N losses of 118.1–155.3 Tg N a⁻¹ in the ORCHIDEE-CN model and Gruber and Galloway (2008) estimate the rate of N losses via leaching and gaseous losses to be 308 Tg N a⁻¹ without and 397 Tg N a⁻¹ with anthropogenic perturbations.

N leaching in the UVic-CN model is more widespread than seen in Yang et al. (2009) with values of 0.5–2 g N m⁻² a⁻¹ in boreal regions, 1–4 g N m⁻² a⁻¹ in temperate regions and 2–4 g N m⁻² a⁻¹ in the tropics with peak values ranging from 4–10 g N m⁻² a⁻¹ (Fig. 5b) compared to 2–6 g N m⁻² a⁻¹ in some tropical and temperate regions and < 1 g N m⁻² a⁻¹ in all other regions in Yang et al. (2009).

3.3 Effect of CN feedbacks on carbon pools and fluxes

Before integrating the UVic model versions transiently, experiments are used to re-adjust the leaf nitrogen values (n_l) used in the C-only version in place of $1/\text{CN}_{\text{leaf}}$ in Eq. (27) in order to achieve a comparable annual gross primary productivity (GPP) in both model versions for the pre-industrial simulations (Table 6). The resulting GPP values for 1800–1849 are 115.8 Pg C a⁻¹ for the C-only and 117.2 Pg C a⁻¹ for the CN-coupled version. Despite the fact that GPP of the C-only version is slightly lower at the

CN feedback in the UVic ESCM

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



beginning of the transient simulation, by the 1990s the GPP of the C-only version is $133.1 \text{ Pg C a}^{-1}$ and therefore higher than in the CN version ($129.6 \text{ Pg C a}^{-1}$) (Table 6). This indicates that N availability has already led to the limitation of GPP in the UVic-CN version by the end of the 20th century. This N limitation of GPP around the end of the 20th century is also found in the CLM4 (Bonan and Levis, 2010) and ORCHIDEE-CN (Zaehle et al., 2010b) models.

Despite similar GPP between the UVic C-only and UVic CN versions for the pre-industrial period, NPP differs between the two versions: 56.4 Pg C a^{-1} (C-only) versus 66.0 Pg C a^{-1} (CN) for the 1800–1849 period and 67.1 Pg C a^{-1} (C-only) versus 75.2 Pg C a^{-1} (CN) for the 1990s. The reason for the difference in NPP values is the dependence of autotrophic respiration on N content in leaf, root and sapwood in the UVic model, which follows Eq. (30) from the original TRIFFID version (Cox et al., 1999)

$$R_m = 0.012 R_d \left(S + \frac{N_{\text{root}} + N_{\text{stem}}}{N_{\text{leaf}}} \right) \quad (30)$$

where 0.012 is a factor to convert units of $\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ to $\text{kg C m}^{-2} \text{ s}^{-1}$. R_m and R_d are the maintenance and dark respiration, respectively, S the soil moisture, and $N_{\text{root}}, N_{\text{stem}}, N_{\text{leaf}}$ are the N contents in root, stem and leaf in kg N kg C .

In UVic C-only, as in the original TRIFFID code, N contents in root and sapwood are calculated in relation to the leaf N content Cox et al. (1999, Eqs. 31–33). In UVic-CN however, N contents are based on explicit N fluxes into and out of the plant tissues and N levels in the plant depend on the availability of N in the environment. This leads to lower sapwood N contents in the CN-coupled version, which leads to lower autotrophic respiration rates, which in turn results in higher NPP values. The effect of this can also be seen in the zonal averaged NPP values in Fig. 6 bottom, left. NPP in the CN-coupled version is higher than the C-only version at latitudes where the vegetation is dominated by trees, i.e. tropics and the boreal region (not considering the 30° S to 60° S latitudinal band, where GPP differs between the C-only and the CN-coupled mode). Although NPP in the UVic-CN model is higher than in CLM4 and ORCHIDEE-CN (Bonan and

CN feedback in the UVic ESCM

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Levis, 2010; Zaehle et al., 2010b), it is still within the range of other model estimates of 55.4–83.8 Pg C a⁻¹ (Arora and Matthews, 2009). Nevertheless, the high NPP/GPP ratio of 0.58 in the CN-coupled version points towards the necessity of re-visiting the autotrophic respiration calculation in TRIFFID.

5 The increase in NPP in the UVic C-only version from 1800 to 1999 is 19 %, whereas it is only 12 % for the CN version. It is still uncertain, how much of an CO₂ fertilisation effect we can expect. Early results from the FACE experiments suggest an increase in productivity by 23±2 % for approximately 550 ppmv CO₂ (Norby et al., 2005), which is also reproduced in a modelling study (Hickler et al., 2008). More recent results
10 from one of the Free Air CO₂ Experiments (FACE) show that the initial increase of NPP of deciduous sweetgum trees due to enhanced CO₂ wore off after an initial 4–5 yr period and dropped from an enhancement effect of 24 % in 2001–2003 to 9 % in 2009, which is hypothesised to be caused by N-limitation (Norby et al., 2010; Garten Jr. et al., 2011), supporting the kind of N limitation seen in models. However, the
15 decrease in NPP in deciduous, and therefore more N-demanding sweetgum, is not reproduced in the evergreen *Pinus taeda* at the Duke FACE experimental site, which showed a continuous enhancement of NPP by 22–30 % (McCarthy et al., 2010).

Over the 1980–1990 period, the zonally averaged GPP values from both model versions are quite close to each other (Fig. 6). The main difference between the two
20 model versions arises between the latitudes 30° S and 60° S. The CN-coupled model simulates lower average GPP values for this part of the Southern Hemisphere than the C-only version, which fit the observed, data derived median GPP values from Beer et al. (2010) better. Both UVic model version simulate a lower, but wider peak around the tropics than the data by Beer et al. (2010) (Fig. 6). The global simulated GPP of
25 the UVic-CN version is in good agreement with the most recent, observation-based, estimate of 123±8 (Beer et al., 2010).

Vegetation carbon stocks are driven by wood density and are highest in tropical forests followed by temperate and boreal forests in the UVic-CN version (Fig. 7 top left). Simulated vegetation C stocks are 12–16 kg C m⁻² for tropical forests and

CN feedback in the UVic ESCM

R. Wania et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

4–12 kg C m⁻² for temperate and boreal forests, which is close to observations that show mean values of 12.1 kg C m⁻² for tropical and 5.7–6.4 for temperate and boreal forests (Malhi et al., 1999). Soil carbon stocks are highest in cold regions where decomposition rates are low (Fig. 7 bottom left). The difference between the UVic-CN and the UVic-C version are shown on the right hand side of Fig. 7. The largest vegetation carbon gains in UVic-CN compared to UVic-C are in the range of 3–5 kg C m⁻² found in the circumpolar region, tropical regions gain less C. Soil carbon gains are highest in cold areas including the circumpolar region and the Tibetan plateau area, which decreases the discrepancy between modelled soil C stocks in the boreal region in UVic-CN and observations, e.g., Malhi et al. (1999) report an average of 34.3 kg C m⁻² for boreal soils and the IGBP-DIS data shows high abundance of gridcells with a soil C content of 30 kg C or more (Global Soil Data Task Group, 2000). Soil C in extra-boreal regions in the UVic-CN version is generally higher than in the UVic-C, which brings the model results closer to observations, which are in the range of 9.6 and 12.3 kg C m⁻² for the temperate and tropical regions, respectively (Fig. 7c,d).

Total global vegetation stocks are higher in the UVic-CN version than in the UVic-C version due to higher NPP (Table 6), for which the reasons are discussed above. This is in contrast to Zaehle et al. (2010b) and Bonan and Levis (2010), who found a decrease in vegetation productivity when including CN interactions in their models and therefore lower vegetation C stocks. The soil C stocks are higher in the UVic-CN version than in the C-only version, which is in agreement with Bonan and Levis (2010) but in disagreement with Zaehle et al. (2010b). In our case, soil C stocks increased when including CN interactions because the consideration of mineral N concentration in Eq. (5) leads to a faster humification process than when not including CN interactions. Higher humification rates mean more input into the soil C pool while at the same time soil decomposition is not influenced by the mineral N concentration (Eq. 13) and does therefore not increase. The faster humification process and with it the faster litter decomposition (Eq. 7) lead to a smaller litter C pool in the UVic-CN version (Table 6).

**CN feedback in the
UVic ESCM**

R. Wania et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

3.4 Historical changes of C fluxes and pools

In Fig. 8 we compare how carbon fluxes and pools in the CN-coupled and the C-only version have evolved over the 19th and 20th century. GPP values of both versions increase over the last two centuries, remaining comparable up to the 1880s, but diverging from then on with the C-only version increasing faster than the CN-coupled version (Fig. 8a). The point of divergence coincides with a change in radiative forcing caused by volcanic eruption of Krakatoa in 1883. Around 1883, both model versions show an increase in GPP followed by a decrease, though the decrease for the C-only version is much smaller than the decrease for the CN-coupled version. This difference in GPP fluctuations following volcanic eruptions can also be seen between 1800 and 1840. After each of the volcanic events, GPP first increases and then drops again. In case of the C-only version, GPP rates drop back to the value observed before the volcanic event, but the GPP in the CN-coupled version shows a much stronger decrease after a preceding spike.

The reason why the UVic ESCM simulates an increase in GPP directly after volcanic eruptions is twofold: On the one hand, air temperature drops after volcanic eruptions due to an increase in aerosols (e.g., Harris and Highwood, 2011), which cause higher carbon assimilation rates in TRIFFID/MOSES (Cox et al., 1999, Eq. 15). On the other hand, soil moisture increases due to a decrease in evaporation that exceeds the decrease in precipitation. Following (Cox et al., 1999, Eq. 18), an increase in soil moisture leads to higher carbon assimilation rates. The difference between the CN-coupled and the C-only version arises from the accumulation of C biomass through increased GPP; the CN-coupled version lags behind in acquiring enough N to maintain stable C/N concentration ratios within the plant tissue and the increase in C/N ratios affects photosynthesis negatively (Eq. 27). Global average C/N ratios in leaves increase during each volcanic event and return to pre-event values afterwards. When comparing NPP (Fig. 8b) to heterotrophic respiration, HR (Fig. 8c) we can see complementary patterns, i.e. when NPP shows a positive anomaly after a volcanic eruption, HR shows a negative one due to the opposite effect of temperature on those two variables. Lower

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



temperature increases GPP and hence NPP in the UVic model, but it decreases soil and litter respiration rates. The CN-coupled and C-only versions show very similar trends up to 1960, when they start diverging for both NPP and HR due to the higher GPP values.

5 The total land C pool shown in Fig. 8f is determined by the soil and litter C pools (Fig. 8e) which are much larger than the vegetation C pool (Fig. 8d). The vegetation C pools of the CN-coupled and C-only version follow each other until 1960; the strong decrease between 1900 and 1960 is due to land use change. The difference between the two model versions is that the vegetation C pool in the C-only version recovers
10 from land use change at the beginning of the 1980s whereas the CN-coupled version does not show a recovery at that point. By the year 1999, the CN-coupled version had lost 13.8 PgC compared to the year 1800, whereas the C-only version had only lost 4.5 PgC. This loss of vegetation C is not observed in the CLM-CN model, which does not consider land use change and where the vegetation pools gain 142.9 PgC (C-only)
15 and 57.4 PgC (CN coupled mode) (Thornton et al., 2007).

The soil and litter C pool anomaly for the CN-coupled model is higher during the the first 150 yr of the simulation, but even though it increases after 1960, it does not increase as fast as the C-only version and the anomaly by the year 1999 is therefore higher for the C-only version (72 PgC) than for the CN-coupled version (60.5 PgC)
20 (Fig. 8e). This pattern also dominates the total C shown in Fig. 8f, which shows that between 1800 and 1960, the terrestrial biosphere gained up to 20 PgC and between 1960 and 1999 it gained another 26–47 PgC depending on the model version. A difference of 21 PgC in total C accumulation by the year 1999 compares well to the ORCHIDEE model, in which the C-only version gained 25 PgC more than the CN-coupled version
25 in the period 1860–2000 (Zaehle et al., 2010a).

The climate sensitivities for the period 1800–1999 β_L and γ_L are listed in Table 7. A previous version of the UVic model had a β_L value of $1.2 \text{ PgC ppmv}^{-1}$ and a γ_L value of -98 PgC K^{-1} (Friedlingstein et al., 2006). The current version of the UVic model simulates a β_L value of 1.2 for the C-only and $0.8 \text{ PgC ppmv}^{-1}$ for the CN-

CN feedback in the UVic ESCM

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



coupled version. The γ_L sensitivity changes from -98 in the previous UVic version to -107 Pg C K^{-1} in the C-only version described here due to the inclusion of the litter pool. The CN-coupled version shows a reduced sensitivity to temperature of -91 Pg C K^{-1} .

The reduction of the β_L sensitivity when including CN interactions is also found in all other models listed in Table 7, though the UVic model shows the smallest reduction in β_L . The C sensitivity to temperature of the UVic model is the highest one compared to other models that have included CN interactions but is lower than the Hadley Centre model in the C4MIP study (Friedlingstein et al., 2006). The change of γ_L when including CN interactions ranges from a decrease in the negative value (UVic ESCM, ORCHIDEE) to a switch from a negative to a positive value (CLM4, IGSM) (Table 7). The strongest effect on γ_L has been found in the IGSM model which is integrated up to the year 2350, which could have an effect on the resulting γ_L values. However, Zaehle et al. (2010a) find that γ_L values stayed relatively stable at least over the 21st century.

3.5 Sensitivity of land C uptake

In order to evaluate the sensitivity of the land C uptake to the introduction of N into the UVic model, we compare the spatial distribution and the zonal averages of Net Ecosystem Production (NEP), i.e. the CO_2 flux from the atmosphere to the land, of the UVic CN-coupled model to the UVic C-only model under different forcing regimes for the 1990s (Fig. 9). The C-only version of the UVic ESCM simulates a strong C sink in tropical regions and a less strong C sink for the extra-tropical regions for the 1990s under the “Fully Forced” experiment (Fig. 9c). Almost all of the Amazon, tropical Africa and parts of Southeast Asia take up C at a rate of over $20 \text{ g C m}^{-2} \text{ a}^{-1}$. A large proportion of these tropical C sinks disappears in the UVic CN-coupled version (Fig. 9b), but the boreal C sinks remain.

Expressed as zonal averages, NEP around the equator shows a reduction from about 0.35 Pg C a^{-1} per 10° latitude in the C-only model to 0.1 Pg C a^{-1} in the CN model (Fig. 9a). Another reduction in the C sink strength is seen in the mid-latitudes,

CN feedback in the UVic ESCM

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



CN feedback in the UVic ESCM

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



between 40° N and 60° N; here, a drop from about 0.2 Pg C a⁻¹ in the C-only model to < 0.1 Pg C a⁻¹ in the CN model is observed. A reduction in NEP in the tropics and the mid-northern latitudes are also observed in the MIT CN-TEM model when compared to the MIT C-TEM model (Sokolov et al., 2008). When comparing our results to the ones from the ORCHIDEE model, we find two main differences though: first, the zonally averaged NEP in both ORCHIDEE versions for the 1990s is larger in mid-latitudes (> 0.4 Pg C a⁻¹) than in low latitudes (< 0.4 Pg C a⁻¹), and second, the zonally averaged NEP south of 50° N in the ORCHIDEE model is higher in the CN version than in the C-only version (Zaehle et al., 2010b), which contrasts the results of the UVic ESCM. This difference indicates that the N effect on the C cycle is stronger in the UVic ESCM than in the ORCHIDEE model.

In the “Fully Forced minus Vegetation” experiment, where the vegetation experiences constant atmospheric CO₂ concentrations at 1800 levels, whereas climate and N deposition are transient, almost all of the land area turns into a C source (Fig. 9d–f). In the C-only version the Amazon is a stronger C source than in the CN-coupled version but the opposite is true for Southeast Asia. When comparing the “Fully Forced” to the “Fully Forced minus Vegetation” experiments a larger decrease of tropical NEP is observed in the C-only version than in the CN version, bringing the NEP values of the C-only and CN version closer to each other between 50° S and 20° N (Fig. 9d). Tropical NEP in the C-only model decreases by 0.39–0.43 Pg C a⁻¹ per 10°-latitude band, whereas the CN version decreases only by 0.20–0.23 Pg C a⁻¹. The stronger reduction in NEP in the C-only compared to the CN version has also been found in the ORCHIDEE model (Zaehle et al., 2010b). In our model, this difference is due to a reduction in NPP that averages 16.4 % between 30° S and 30° N in the C-only version but only 12.9 % in the CN-coupled version.

The “Fully Forced minus Climate” experiment, basically a CO₂ fertilisation experiment, results in an increase of NEP compared to the “Fully Forced” experiment in the C-only version between 30° S and 60° N, with the strongest increase around the equator of 0.12 Pg C a⁻¹ per 10°-latitude band (Fig. 9g–i). In contrast, the CN-coupled version

does not show increases of NEP around the equator, but rather in mid-latitudes, i.e. 10° S–30° S and 40° N–50° N.

The last experiment, “Fully Forced minus N deposition” is similar to the Fully Forced experiment, only that N deposition is excluded from the model. As the zonal average shows, the simulation without N deposition has a reduced C sink strength between 10° S and 60° N, in the areas where N deposition happens (Dentener, 2006). Zaehle et al. (2010b) found that the latitudes between 35° N and 65° N are most affected by N deposition in the ORCHIDEE-CN model. The sensitivity of the UVic model to N deposition in the tropics together with the lack of increase in NEP in the “Fully Forced minus Climate” experiment is likely to be related to changes in the Amazon basin.

Throughout the figures, the Amazon basin is different from other tropical regions with lower ammonium and nitrate concentration (Fig. 4), lower plant uptake (Fig. 5a), partially in GPP and NPP (Fig. 6). One difference between the Amazon and the rest of the tropics that we have found is a much higher simulated soil moisture. Higher soil moisture leads to higher runoff and despite lower ammonium and nitrate concentrations, leaching rates of mineral N are about the same in the Amazon as in other tropical regions (Fig. 5b), which means that in our model relatively more mineral N is lost via leaching in the Amazon than in other regions. Lower soil ammonium and nitrate concentrations cause lower plant uptake rates, leading to higher leaf C/N ratios in the Amazon, which lowers photosynthesis.

Global numbers for NEP are given in Table 8. The difference in NEP between the C-only (FF2) and the CN-coupled (FF2) is 0.74 Pg C a⁻¹ in the “Fully Forced” simulations. This drop in NEP is simulated despite the increase in NPP in the CN-coupled version discussed above; the lower NEP is caused by higher soil and litter respiration rates reducing the C sink strength in the CN-coupled version. A drop of 0.7 Pg C a⁻¹ from the C-only to the CN-coupled version is also found in the CLM4 model (Bonan and Levis, 2010).

CN feedback in the UVic ESCM

R. Wania et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



CN feedback in the UVic ESCM

R. Wania et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



The model experiments “Fully Forced minus Vegetation” result the land to become a strong C source in both model versions. The land in the C-only version represents a slightly stronger C source ($-0.63 \text{ Pg C a}^{-1}$) than the one in the CN-coupled version ($-0.60 \text{ Pg C a}^{-1}$). The difference between the CN-coupled version and the C-only version in the UVic model is smaller than that found by Zaehle et al. (2010b, approximately -0.7 Pg C a^{-1} for the ORCHIDEE-C and -0.3 for ORCHIDEE-CN).

When the model is integrated in the “Fully Forced minus Climate” mode, we observe a larger increase in global NEP in the C-only model (from 1.57 to 2.17 Pg C a^{-1}) than in the CN-coupled version (from 0.83 to 1.05 Pg C a^{-1}) compared to the “Fully Forced” simulations (Table 8). The global effect of excluding N deposition is a reduction of the annual NEP from 0.83 Pg C a^{-1} to 0.48 Pg C a^{-1} or expressed as the positive effect of anthropogenic N deposition, we find an enhancement of NEP of 0.35 Pg C a^{-1} , which falls in the range of the estimates by Zaehle et al. (2010b) of 0.2 – 0.5 Pg C a^{-1} .

When looking at the linearity of the additive effect of the climate experiments (E1 + E2 and E4 + E5) and compare them to the fully forced simulations (FF1 and FF2) we find a strong non-linearity in the CN-coupled version ($\text{FF1} \neq \text{E1} + \text{E2}$, i.e. $0.83 \neq 0.45 \text{ Pg C a}^{-1}$) but only a weak non-linearity in the C-only version ($\text{FF2} \approx \text{E4} + \text{E5}$, i.e. $1.57 \approx 1.54 \text{ Pg C a}^{-1}$) (Table 8). A similar non-linearity has been found in the ORCHIDEE-CN by Zaehle et al. (2010b), who compared their “Fully Forced” version to the “Fully Forced minus Vegetation” + “Fully Forced minus Climate” (all three versions are without N deposition) and got a difference of 0.4 Pg C a^{-1} , i.e. the NEP of the “Fully Forced” is 0.4 Pg C a^{-1} higher than the arithmetic sum of the other two simulations. In our case, that difference is 0.38 Pg C a^{-1} .

4 Conclusions

The UVic ESCM follows a suite of other Earth System Models that have included terrestrial CN-feedbacks. There is large uncertainty around some of the relevant pool sizes (e.g. N pool in vegetation, NO_3^- pool in soils) and flux strengths (e.g. N uptake

**CN feedback in the
UVic ESCM**

R. Wania et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

or leaching), which cannot be eliminated until we have gathered better data. The UVic ESCM agrees with some models and disagrees with others but shows in general a similar behaviour to other CN-coupled models; where disagreement happened, we found an explanation for the different behaviour between our model and others. One of the main attributes of the UVic CN-coupled ESCM is that the inclusion of N leads to an increase of the NPP:GPP ratio which is caused by a reduction in autotrophic respiration due to its relationship with plant N content. Even though the current formulation of the autotrophic respiration served the C-only version well, the high NPP:GPP ratio suggests that it is unrealistic for a CN-coupled version and should be replaced in a future version.

The high soil moisture contents in the Amazonian basin are the reason why this region stands out compared to other tropical regions. Higher soil moisture contents lead to faster microbial processes, causing low mineral N concentrations. The Amazonian basin shows lower productivity values and a nearly neutral NEP and only minor changes in our forcing experiments. The overall cause for the high soil moisture values in the Amazon is a bias towards high precipitation in that region in the UVic ESCM.

Similar to other models, we find that the coupling of the C and N cycle leads to reductions in the NEP under fully forced conditions and it introduces a strong non-linear behaviour of NEP. This non-linearity arises either from a mitigated negative effect of temperature on NEP or a suppressed positive effect of CO₂ on NEP.

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CN feedback in the UVic ESCM

R. Wania et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[◀](#)

[▶](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



CN feedback in the UVic ESCM

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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**CN feedback in the
UVic ESCM**

R. Wania et al.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[◀](#)
[▶](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


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**CN feedback in the
UVic ESCM**

 R. Wania et al.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[◀](#)
[▶](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


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**CN feedback in the
UVic ESCM**

R. Wania et al.

[Title Page](#)
[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

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CN feedback in the UVic ESCM

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Table 1. Pools and fluxes in the UVic-CN model.

Variable	Units	Description
Carbon		
C_L	kg C m^{-2}	Litter C pool
C_S	kg C m^{-2}	Soil C pool
C_{leaf}	kg C m^{-2}	PFT-dependent leaf C pool
C_{root}	kg C m^{-2}	PFT-dependent root C pool
C_{wood}	kg C m^{-2}	PFT-dependent wood C pool
C_{LF}	$\text{kg C m}^{-2} \text{ a}^{-1}$	C litterfall
C_{HUM}	$\text{kg C m}^{-2} \text{ a}^{-1}$	C humification, i.e. transfer from litter to soil
C_{RESPL}	$\text{kg C m}^{-2} \text{ a}^{-1}$	Litter C respiration, i.e. transfer from litter to atmosphere
C_{RESPS}	$\text{kg C m}^{-2} \text{ a}^{-1}$	Soil C respiration, i.e. transfer from soil to atmosphere
C/N ratios		
CN_{leaf}	kg C (kg N)^{-1}	PFT-dependent leaf C/N ratio
CN_{root}	kg C (kg N)^{-1}	PFT-dependent root C/N ratio
CN_{wood}	kg C (kg N)^{-1}	PFT-dependent wood C/N ratio
Organic nitrogen		
M_L	kg N m^{-2}	Litter N pool
M_S	kg N m^{-2}	Soil N pool
M_V	kg N m^{-2}	Vegetation N pool
M_{LF}	$\text{kg N m}^{-2} \text{ a}^{-1}$	N litterfall
M_{HUM}	$\text{kg N m}^{-2} \text{ a}^{-1}$	N humification, i.e. transfer from litter to soil
M_{MINL}	$\text{kg N m}^{-2} \text{ a}^{-1}$	Litter N mineralisation, i.e. transfer from litter to NH_4^+ pool
M_{MINS}	$\text{kg N m}^{-2} \text{ a}^{-1}$	Soil N mineralisation, i.e. transfer from soil to NH_4^+
Mineral nitrogen		
NH_4	kg N m^{-2}	NH_4^+ pool
NH_4^{DEP}	$\text{kg N m}^{-2} \text{ a}^{-1}$	NH_4^+ deposition
NH_4^{UP}	$\text{kg N m}^{-2} \text{ a}^{-1}$	NH_4^+ uptake
NH_4^{IMM}	$\text{kg N m}^{-2} \text{ a}^{-1}$	NH_4^+ immobilisation
NH_4^{LEA}	$\text{kg N m}^{-2} \text{ a}^{-1}$	NH_4^+ leaching
BNF	$\text{kg N m}^{-2} \text{ a}^{-1}$	Biological N_2 fixation
NO_3	kg N m^{-2}	NO_3^- pool
NO_3^{DEP}	$\text{kg N m}^{-2} \text{ a}^{-1}$	NO_3^- deposition
NO_3^{UP}	$\text{kg N m}^{-2} \text{ a}^{-1}$	NO_3^- uptake
NO_3^{IMM}	$\text{kg N m}^{-2} \text{ a}^{-1}$	NO_3^- immobilisation
NO_3^{LEA}	$\text{kg N m}^{-2} \text{ a}^{-1}$	NO_3^- leaching
NIT	$\text{kg N m}^{-2} \text{ a}^{-1}$	Nitrification

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



CN feedback in the UVic ESCM

R. Wania et al.

Table 2. List of PFT-dependent parameters used in UVic ESCM-CN: Leaf base turnover rate (η_{leaf}^0), root turnover rate (η_{root}) and wood turnover rate (η_{wood}) are all taken from the UVic ESCM, and retranslocation of N before leaf abscission (r_{leaf}) and maximum N uptake rate (v_{max}) are taken from Gerber et al. (2010). Minimum and maximum C/N ratios for leaves ($\text{CN}_{\text{Leaf,min}}$, $\text{CN}_{\text{Leaf,max}}$) and roots ($\text{CN}_{\text{Root,min}}$, $\text{CN}_{\text{Root,max}}$) for each PFT are chosen as follows: $\text{CN}_{\text{Leaf,min}}$ are the inverted maximum leaf N concentrations used in the previous UVic ESCM (Meissner et al., 2003) with the exception of the value for C3G which is raised from 18 to 25. $\text{CN}_{\text{Leaf,max}}$ are allocated in order to allow a wide range of possible CN ratios, $\text{CN}_{\text{Root,min}}$ and $\text{CN}_{\text{Root,max}}$ are set to be higher than $\text{CN}_{\text{Leaf,min}}$ and $\text{CN}_{\text{Leaf,max}}$ (White et al., 2000). Average leaf nitrogen concentration, n_1 , is used in the C-only version to calculate Rubisco activity $V_{\text{c,max}}$. BT = broad-leaved trees, NT = needle-leaved trees, C3G = C₃ grasses, C4G = C₄ grasses, SH = shrubs.

Parameter	Unit	BT	NT	C3G	C4G	SH
η_{leaf}^0	a^{-1}	0.25	0.25	0.25	0.25	0.25
η_{root}	a^{-1}	0.25	0.25	0.25	0.25	0.25
η_{wood}	a^{-1}	0.01	0.01	0.20	0.20	0.05
r_{leaf}	–	0.5	0.4	0.5	0.5	0.5
v_{max}	$\text{kg N (kg root C)}^{-1} \text{ a}^{-1}$	0.0054	0.0054	0.072	0.072	0.072
$\text{CN}_{\text{Leaf,min}}$	kg C (kg N)^{-1}	28	33	25	37	37
$\text{CN}_{\text{Leaf,max}}$	kg C (kg N)^{-1}	70	80	60	80	80
$\text{CN}_{\text{Root,min}}$	kg C (kg N)^{-1}	40	50	30	40	50
$\text{CN}_{\text{Root,max}}$	kg C (kg N)^{-1}	80	90	70	85	90
$1/n_1$	kg C (kg N)^{-1}	37	46	25	46	37

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[I◀](#)
[▶I](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


CN feedback in the UVic ESCM

R. Wania et al.

Table 3. List of parameters used in the UVic ESCM model that are either new or have changed values.

Parameter	Value	Units	Description	Used in	Source
ξ	45	$\text{m}^3 \text{kg N}^{-1}$	Modifier of litter decomposition rate	Eqs. (5)–(8)	Gerber et al. (2010)
τ	0.42	–	Fraction of decomposition transferred to soil pool	Eqs. (5)–(8)	tuned ¹
k_L	1.419	a^{-1}	Litter turnover rate at 25 °C	Eqs. (5)–(8)	tuned ¹
k_S	0.047	a^{-1}	Soil turnover rate at 25 °C	Eqs. (13)–(14)	tuned ¹
$k_{p,1/2}$	0.003	kg N m^{-3}	Half-saturation constant for N uptake	Eqs. (17)–(18)	Gerber et al. (2010)
h_S	1	m	Soil depth	Eqs. (17)–(18)	UVic ESCM
k_{Nit}	51.6	a^{-1}	Maximum nitrification rate adjusted to 25 °C	Eq. (21)	Xu-Ri and Prentice (2008)
ϵ	0.0027	kg N (kg C)^{-1}	Relationship between BNF and NPP	Eq. (23)	Derived from UVic-CN
b_{NH_4}	10	–	Sorption/desorption buffer factor for NH_4	Table 4	Gerber et al. (2010)
b_{NO_3}	1	–	Sorption/desorption buffer factor for NO_3	Table 4	Gerber et al. (2010)

¹These three parameters are tuned together in order to obtain a similar value for the sum of soil C and litter C compared to the UVic ESCM v2.9 that has only a soil C pool.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


CN feedback in the UVic ESCM

R. Wania et al.

Table 4. Relationship between different expressions of mineral N pools and concentrations. Values for h_S , b_{NH_4} and b_{NO_3} can be found in Table 3.

Variable	Derived from	Units	Description
NH_4		kg N m^{-2}	NH_4^+ pool
$\text{NH}_{4(\text{av})}$	$\text{NH}_4/b_{\text{NH}_4}$	kg N m^{-2}	Available NH_4^+ pool
$[\text{NH}_4]$	NH_4/h_S	kg N m^{-3}	NH_4^+ concentration
$[\text{NH}_{4(\text{av})}]$	$[\text{NH}_4]/b_{\text{NH}_4}$	kg N m^{-3}	Available NH_4^+ concentration
NO_3		kg N m^{-2}	NO_3^- pool
$\text{NO}_{3(\text{av})}$	$\text{NO}_3/b_{\text{NO}_3}$	kg N m^{-2}	Available NO_3^- pool
$[\text{NO}_3]$	NO_3/h_S	kg N m^{-3}	NO_3^- concentration
$[\text{NO}_{3(\text{av})}]$	$[\text{NO}_3]/b_{\text{NO}_3}$	kg N m^{-3}	Available NO_3^- concentration
$N_{\text{min}(\text{av})}$	$\text{NO}_{3(\text{av})} + \text{NH}_{4(\text{av})}$	kg N m^{-2}	Available mineral N pool
$[N_{\text{min}(\text{av})}]$	$[\text{NO}_{3(\text{av})}] + [\text{NH}_{4(\text{av})}]$	kg N m^{-3}	Available mineral N concentration

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



CN feedback in the UVic ESCM

R. Wania et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[I◀](#)

[▶I](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



Table 5. Description of the UVic ESCM experiments and the forcings used. “FF” are the fully forced simulations and “E” are the experimental simulations in which the forcings are modified. In the forcing column, “FF” indicates a fully forced model, using transient CO₂ concentration for the vegetation and climate and N deposition, “FF minus Vegetation” means that the CO₂ concentration for the vegetation is held constant, “FF minus Climate” means that the CO₂ concentration for the climate is held constant and “FF minus Ndep” means that the N deposition is held constant. “CN” indicates the use of the UVic CN-coupled version and “C-only” indicates the use of the UVic C-only version, “CO₂ for the vegetation/climate” gives the year or period that is used and Ndep gives the year or period of natural and anthropogenic N deposition.

Label	Forcing	UVic ESCM version	CO ₂ for vegetation	CO ₂ for climate	Ndep
FF1	FF	CN	1800–1999	1800–1999	1800–1999
FF2	FF	C-only	1800–1999	1800–1999	–
E1	FF minus Vegetation	CN	1800	1800–1999	1800–1999
E2	FF minus Climate	CN	1800–1999	1800	1800–1999
E3	FF minus Ndep	CN	1800–1999	1800–1999	1800
E4	FF minus Vegetation	C-only	1800	1800–1999	–
E5	FF minus Climate	C-only	1800–1999	1800	–

CN feedback in the UVic ESCM

R. Wania et al.

Table 6. Mean 1990s global fluxes and stocks of C and N as simulated by the UVic-C and UVic-CN versions driven by CO₂ concentrations. The arrows indicate increases (↗) or decreases (↘) when switching CN feedbacks on.

Pool/Flux	UVic-C	UVic-CN	Other CN models results	Reference
Vegetation C (Pg C)	538.5 ↗	635.4	845 (C) ↘ 766 (CN) 647.1 (C) ↘ 537.0 (CN)	Bonan and Levis (2010) Zaehle et al. (2010b)
Litter C (Pg C)	103.9 ↘	81.9	729 (C) ↗ 750 (CN)	Bonan and Levis (2010)
Soil C (Pg C)	1255 ↗	1471	1723.1 (C) ↘ 1288.7 (CN)	Zaehle et al. (2010b)
GPP (Pg C a ⁻¹)	133.1 ↘	129.6	167 (C) ↘ 163 (CN) 148.4 (C) ↘ 132.6 (CN)	Bonan and Levis (2010) Zaehle et al. (2010b)
NPP (Pg C a ⁻¹)	67.1 ↗	75.2	58 (C) ↘ 57 (CN) 65.9 (C) ↘ 57.5 (CN)	Bonan and Levis (2010) Zaehle et al. (2010b)
NEP (Pg C a ⁻¹)	1.53 ↘	0.83	2.5 (C) ↘ 1.8 (CN)	Bonan and Levis (2010)
NEP no land-use (Pg C a ⁻¹)	3.66 ↘	2.93	2.62 (C) ↘ 2.38 (CN)	Zaehle et al. (2010b), Zaehle et al. (2010b)
Vegetation N (Pg N)	–	2.94	3.8	
Litter N (Pg N)	–	1.00		
Soil N (Pg N)	–	113.0	100	Zaehle et al. (2010b)
N uptake (Tg N a ⁻¹)	–	873.2	1126.9	Zaehle et al. (2010b)
N loss (Tg N a ⁻¹)	–	222.8	118.1–155.3	Zaehle et al. (2010b)

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[⏪](#)
[⏩](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


CN feedback in the UVic ESCM

R. Wania et al.

Table 7. Climate sensitivities β_L in (Pg C ppmv^{-1}) and γ_L in (Pg C K^{-1}) of the land C pool in the UVic C-only and CN-coupled version compared to other models.

Model	β_L	γ_L	Year	Reference
UVic ESCM C-only	1.2	−107	1999	this study
UVic ESCM CN-coupled	0.8	−91	1999	this study
ORCHIDEE C-only	1.9	−48	2000	Zaehle et al. (2010a)
ORCHIDEE CN-coupled	1.2	−35	2000	Zaehle et al. (2010a)
CLM3 CN-coupled	0.7	10	2000	Thornton et al. (2009)
CLM4 C-only	0.9	−11 to −12	2004	Bonan and Levis (2010)
CLM4 CN-coupled	0.4 ¹	5 to 6	2004	Bonan and Levis (2010)
IGSM C-only SP1000 ²	1.6	−82	2350	Sokolov et al. (2008)
IGSM CN-coupled SP1000	0.7	4	2350	Sokolov et al. (2008)
IGSM C-only SP550 ²	2.0	−78	2350	Sokolov et al. (2008)
IGSM CN-coupled SP550	0.8	5	2350	Sokolov et al. (2008)
Various C-only models	0.2 to 2.8	−20 to −177	2100	Friedlingstein et al. (2006)

¹: This is the value for the simulation labelled $\text{CN}_{\text{ndep}} + (\Delta\Delta\text{C}_L^{\text{NDEP}})$.

²: SP1000 and SP550 are Bern emission scenarios used in Sokolov et al. (2008).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



CN feedback in the UVic ESCM

R. Wania et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[I◀](#)

[▶I](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



Table 8. Global NEP (Pg C a^{-1}) values for the 1990s.

Forcing	Experiment	CN-coupled	Experiment	C-only
Fully Forced	FF1	0.83	FF2	1.57
Fully Force minus Vegetation	E1	-0.60	E4	-0.63
Fully Force minus Climate	E2	1.05	E5	2.17
Fully Force minus N deposition	E3	0.48		

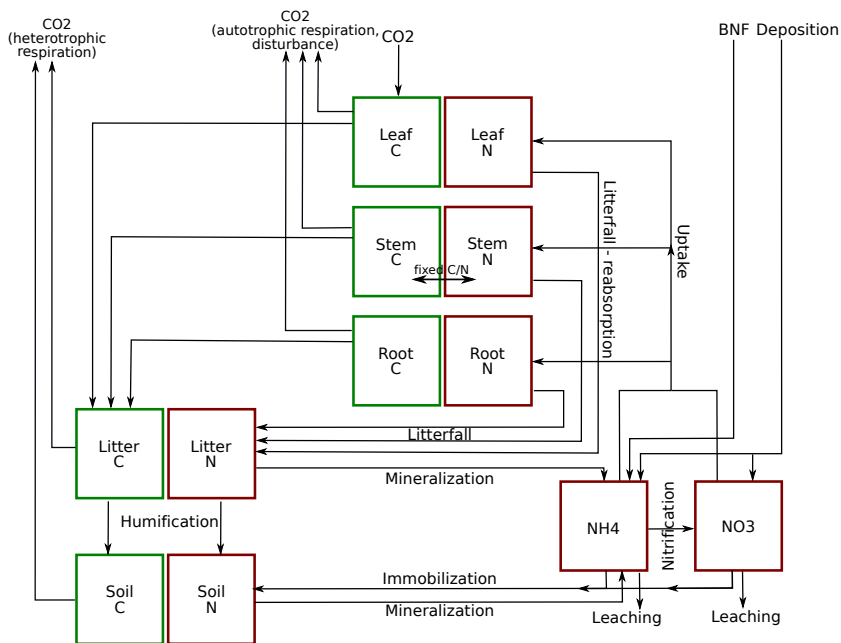


Fig. 1. Schematic representation of the carbon (green boxes) and nitrogen pools and fluxes (red boxes) in the UVic-CN model. The C cycle in the UVic model is enhanced by adding a carbon litter pool. The nitrogen model is adapted from Gerber et al. (2010). Leaf, stem and root N content depend on the size of the C pools and fixed C/N ratios. The UVic inherent leaf, root and stem turnover rates are used to calculate litterfall with the only modification that N in leaves is partially reabsorbed before abscission. The litterfall goes first into the litter pool, which is partially decomposed and enters the NH_4 pool and part of it is humified and enters the soil N pool. The soil N pool is mineralised and adds to the NH_4 pool. Ammonium is turned into NO_3^- via nitrification. Ammonium and NO_3^- can be immobilised by the soil pool. Both of the inorganic N species can be leached via runoff or taken up by plants. The plant uptake is set to meet the PFT's requirement to achieve at least the minimum N content.

CN feedback in the UVic ESCM

R. Wania et al.

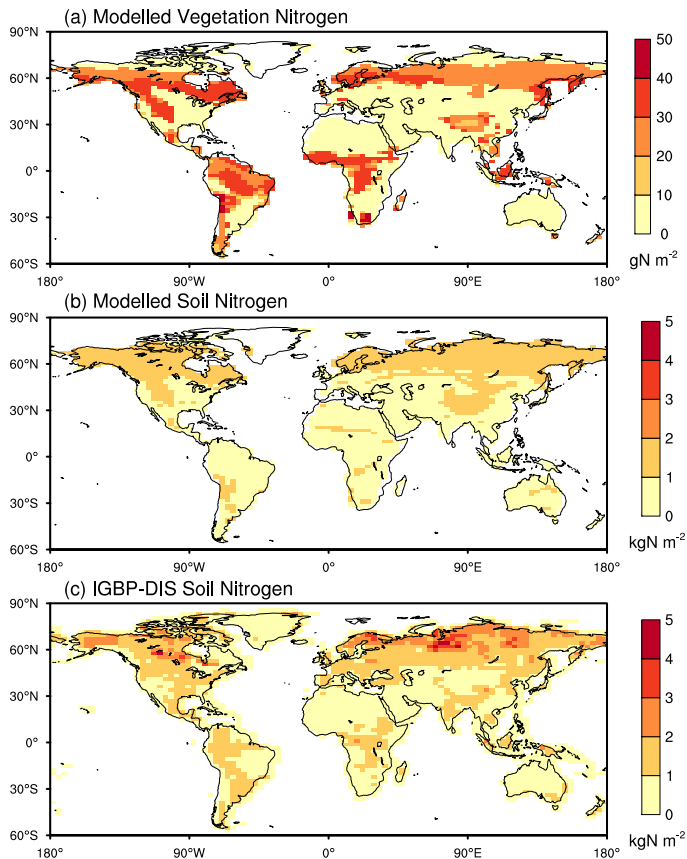


Fig. 2. Mean 1980–1999 nitrogen content in vegetation (a) and soil plus litter (b) simulated by UVic-CN and soil nitrogen content as given by the IGBP-DIS data base (Global Soil Data Task Group, 2000) (c).

Title Page

Abstract Introduction

Conclusions References

Tables Figures

⏪ ⏩

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**CN feedback in the
UVic ESCM**

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

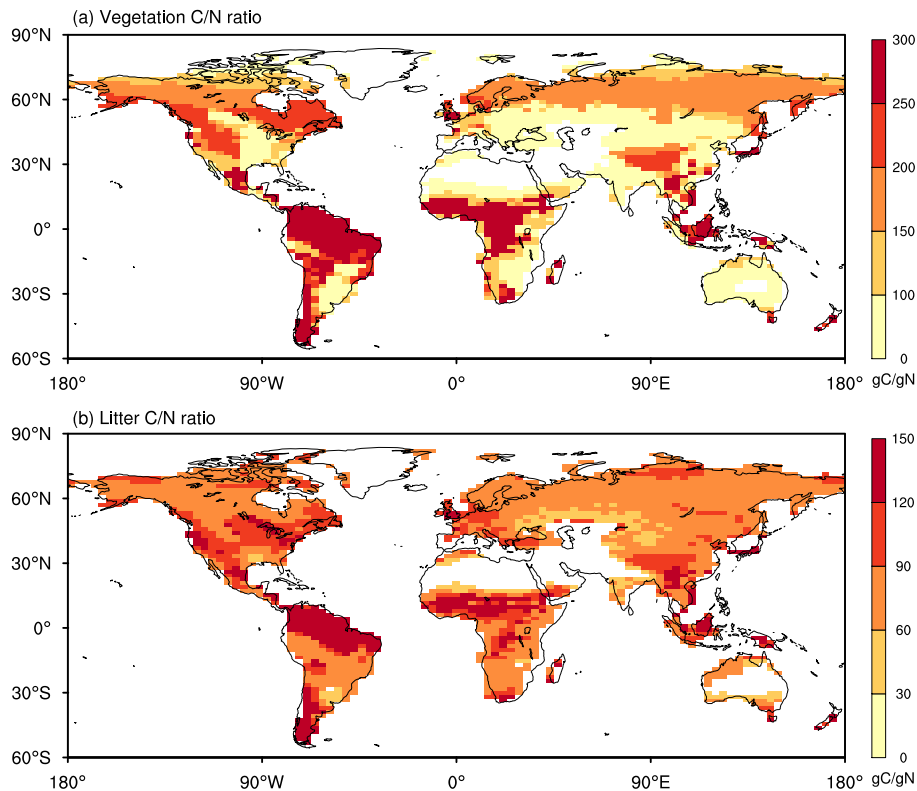
Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

**Fig. 3.** Mean 1980–1999 C/N ratios of vegetation (a) and litter (b) simulated by UVic-CN.

CN feedback in the
UVic ESCM

R. Wania et al.

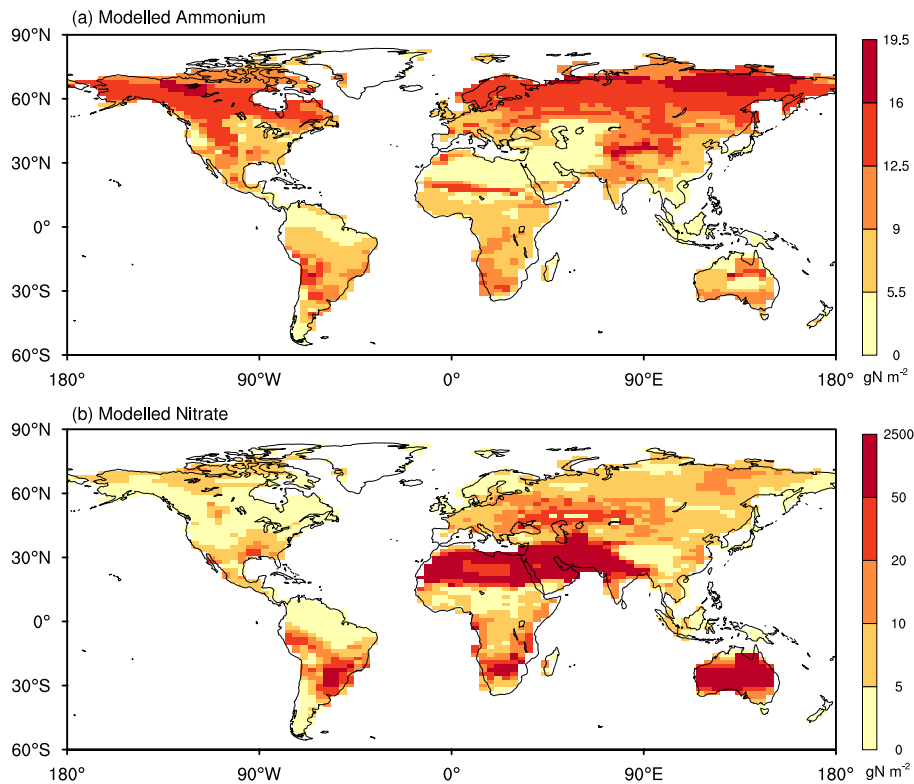


Fig. 4. Mean 1980–1999 ammonium (a) and nitrate (b) pools in the soil simulated by UVic-CN.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

CN feedback in the
UVic ESCM

R. Wania et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

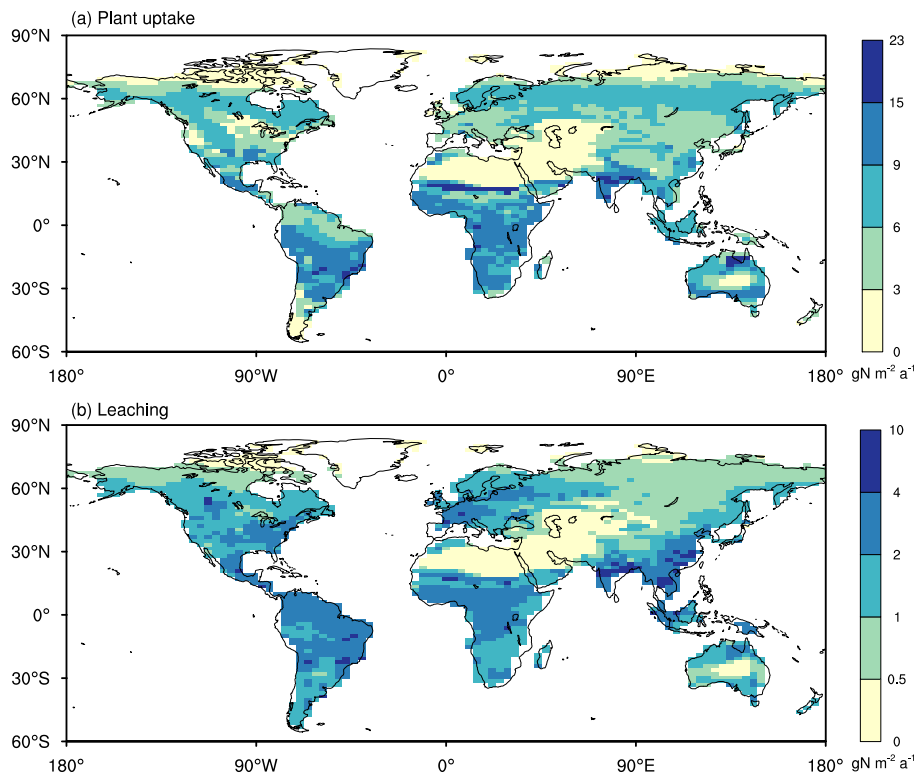


Fig. 5. Mean 1980–1999 plant uptake (a) and leaching (b) of nitrogen simulated by UVic-CN.

CN feedback in the
UVic ESCM

R. Wania et al.

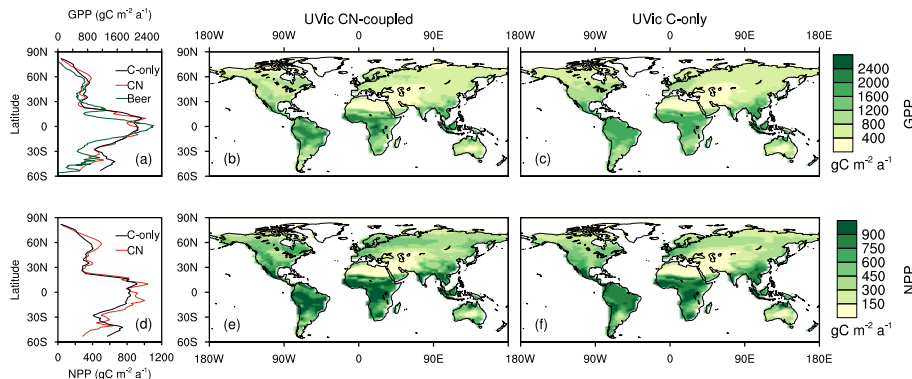


Fig. 6. Mean 1980–1999 gross primary production (GPP) (top row) and net primary production (NPP) (bottom row) for the UVic C-only and UVic-CN version. The line graphs on the left hand side are zonal averages of the UVic C-only (black), the UVic CN-coupled (solid red) data shown in the maps per 1.8° latitude and the median data-driven zonally averaged GPP values taken from Beer et al. (2010) (green).

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[⏪](#)
[⏩](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


CN feedback in the
UVic ESCM

R. Wania et al.

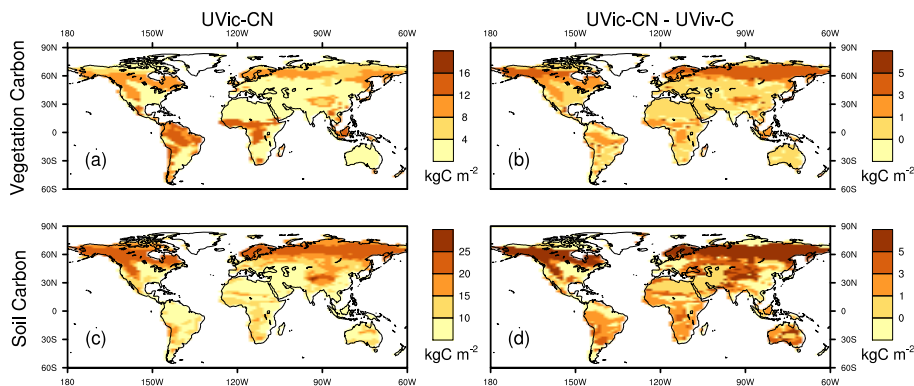


Fig. 7. Mean 1980–1999 carbon content in vegetation (a) and soil plus litter (c) for the UVic-CN simulation (left) and the difference between UVic-CN and UVic-C (right) for vegetation (b) and soil plus litter (d).

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[I◀](#)[▶I](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

CN feedback in the UVic ESCM

R. Wania et al.

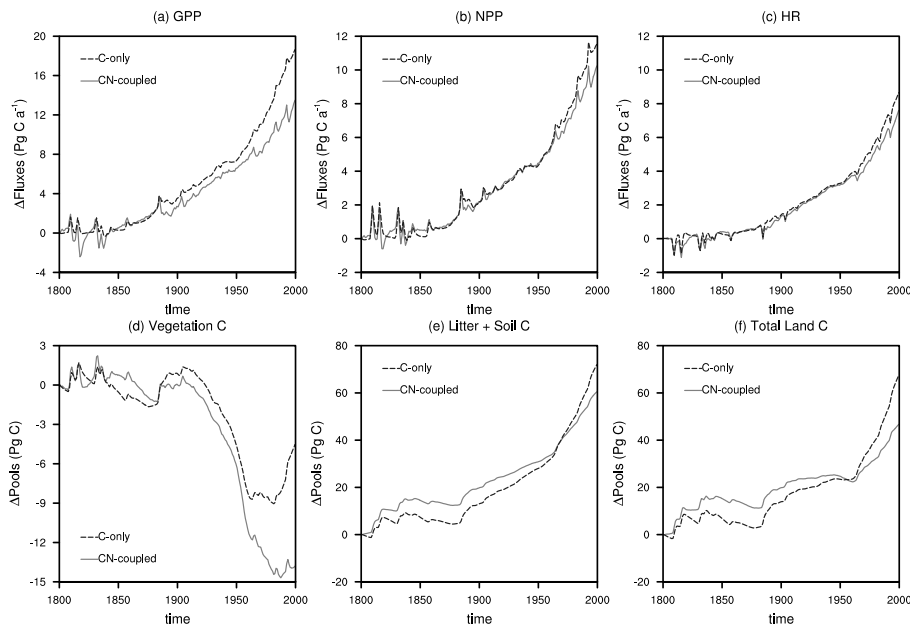


Fig. 8. Changes of carbon fluxes from 1800 to 2000: **(a)** GPP=gross primary production, **(b)** NPP = net primary production and **(c)** HR = heterotrophic respiration and changes of carbon pools **(d)** vegetation, **(e)** litter plus soil and **(d)** total, i.e. the sum of **(d)** and **(e)** for the UVic CN-coupled (grey solid line) and UVic C-only (black dashed line) simulations.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[⏪](#)
[⏩](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

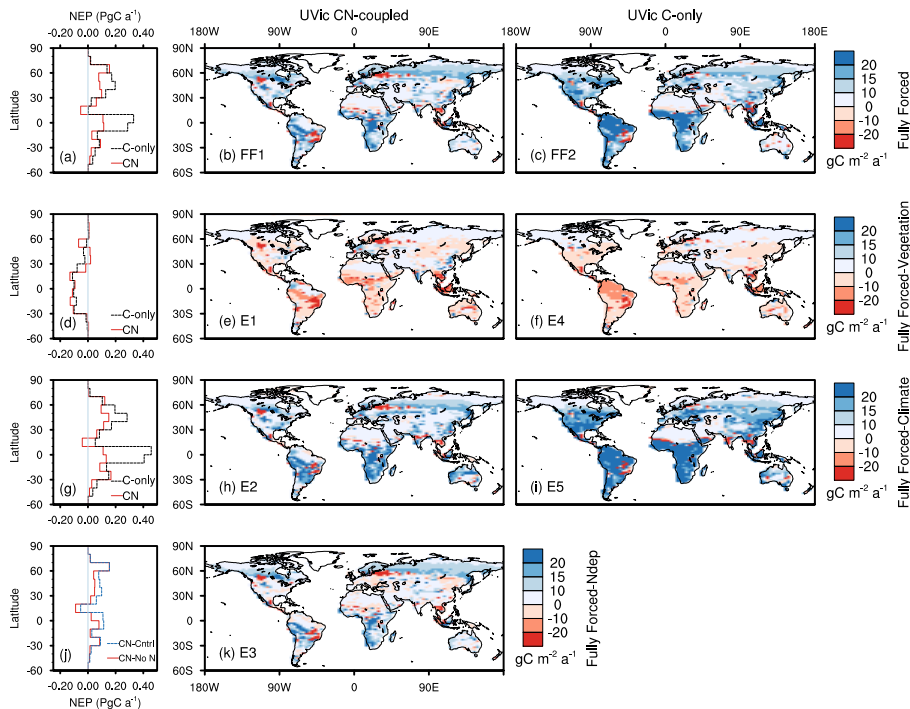



Fig. 9. Mean 1990–1999 Net Ecosystem Production (NEP); positive values indicate a C sink, negative values a C source. Zonal averages of NEP for UVic-CN (solid red) and the UVic C-only version (dashed black) in 10° increments (**a**, **d**, **g**) and spatial distribution of NEP for the CN-coupled version (**b**, **e**, **h**, **k**) and C-only version (**c**, **f**, **i**). In plot (**j**) the UVic-CN “Fully Forced-N dep” (solid red, “CN-No N”) is compared to the UVic-CN “Fully Forced” (blue dashed, “CN cntrl”). Four sets of experiments are shown: “Fully Forced” (FF1 and FF2), “Fully Forced-Vegetation” (E1 for CN and E4 for C-only), “Fully Forced-Climature” (E2 for CN and E5 for C-only) and “Fully Forced-N dep” (E3). See Table 5 for the description of the experiments.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

