



Effects of experimental nitrogen deposition on peatland carbon pools and fluxes: a modelling analysis

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Received: 16 May 2014 – Published in Biogeosciences Discuss.: 1 July 2014

Revised: 1 November 2014 – Accepted: 14 November 2014 – Published: 7 January 2015

Abstract. Nitrogen (N) pollution of peatlands alters their carbon (C) balances, yet long-term effects and controls are poorly understood. We applied the model PEATBOG to explore impacts of long-term nitrogen (N) fertilization on C cycling in an ombrotrophic bog. Simulations of summer gross ecosystem production (GEP), ecosystem respiration (ER) and net ecosystem exchange (NEE) were evaluated against 8 years of observations and extrapolated for 80 years to identify potential effects of N fertilization and factors influencing model behaviour. The model successfully simulated moss decline and raised GEP, ER and NEE on fertilized plots. GEP was systematically overestimated in the model compared to the field data due to factors that can be related to differences in vegetation distribution (e.g. shrubs vs. graminoid vegetation) and to high tolerance of vascular plants to N deposition in the model. Model performance regarding the 8-year response of GEP and NEE to N input was improved by introducing an N content threshold shifting the response of photosynthetic capacity (GEP_{max}) to N content in shrubs and graminoids from positive to negative at high N contents. Such changes also eliminated the competitive advantages of vascular species and led to resilience of mosses in the long-term. Regardless of the large changes of C fluxes over the short-term, the simulated GEP, ER and NEE after 80 years depended on whether a graminoid- or shrub-dominated system evolved. When the peatland remained shrub-*Sphagnum*-dominated, it shifted to a C source after only 10 years of

fertilization at $6.4 \text{ g N m}^{-2} \text{ yr}^{-1}$, whereas this was not the case when it became graminoid-dominated. The modelling results thus highlight the importance of ecosystem adaptation and reaction of plant functional types to N deposition, when predicting the future C balance of N-polluted cool temperate bogs.

1 Introduction

Atmospheric nitrogen deposition has been rapidly increasing since the 19th century owing to human activities such as fertilizer manufacturing and fossil-fuel combustion. Despite declining deposition of oxidized N (NO_x), owing to regulations during the last two decades in Europe and North America, deposition of reduced N (NH_x) that originates from food production remains high (Templer et al., 2012; Rogora et al., 2012; Verstraeten et al., 2012). Globally, N deposition has been projected to increase in many regions until 2100, especially in regions with intense agricultural land use (Lamarque et al., 2011). As a key limiting nutrient for primary production in terrestrial ecosystems (LeBauer and Treseder, 2008), elevated atmospheric N deposition affects the global C cycling and the net sequestration of C (Townsend et al., 1996). Nitrogen deposition was estimated to have caused an increase in global C sequestration of 0.2 Gt C yr^{-1} , accounting for approximately one-fifth of the terrestrial annual net C

uptake between 1996 and 2005 (Zaehle et al., 2011). Northern peatlands have served as a major terrestrial C sink in the Holocene and currently store 547 (473–621) Gt C (Yu et al., 2010), representing about one-third of the global C pool. Long-term C accumulation rates of northern peatlands, which are the residue of the fluxes of gross ecosystem production (GEP) and ecosystem respiration (ER), are relatively small and range from 3 to 71 g C m⁻² yr⁻¹ (Yu et al., 2009) with an average of 23 g C m⁻² yr⁻¹ (Loisel et al., 2014). This C sink function of peatlands, which has been sustained over millennia, may be under risk when N deposition induces changes in the C cycle. For example, a dynamic global vegetation model has simulated a reduction of the maximum annual net primary production in northern peatlands from 800 g C m⁻² yr⁻¹ to 450 g C m⁻² yr⁻¹ when coupling a dynamic N cycle to the C cycle (Spahni et al., 2013).

Current evidence regarding this issue is ambiguous in many aspects. Recent C sequestration rates have been observed to increase in pristine Canadian peatlands undergoing long-term increase of N deposition (Turunen et al., 2004) but to decrease in European bogs (Bragazza et al., 2006) and Alaskan tundra (Mack et al., 2004). Nitrogen is an essential constituent of the carboxylation enzyme (e.g. Rubisco), the light capturing tissues and the plant biomass in general (Evans, 1989, Hikosaka and Terashima, 1995). The maximum leaf photosynthetic rate (GEP_{max}) was found to be strongly and positively related to the leaf N content across C₃ plants (Evans et al., 1989). In extremely nutrient-limited environments, such as peatlands, plants were observed to optimize their growth by increasing nitrogen-use-efficiencies (Small, 1972, Aerts et al., 1999). As adaptations to the N-poor environment, characteristic plant traits emerged, such as slow nitrogen cycling (Urban et al., 1988), small nutrient investment in the photosynthetically active tissue (Wang and Moore, 2014) and large N resorption efficiencies (Wang et al., 2014). The optimization of the growth confounds the effect of N on the photosynthetic capacity and C assimilation of peatland plants. The C assimilation of peatland species was found to be stimulated (Lund et al., 2010), or to remain unaffected (Currey et al., 2011; Gerdol et al., 2008; Bubier et al., 2011) by N enrichment.

Also, the effects of N deposition on ecosystem respiration are uncertain. A meta-analysis suggested a decline of respiration in recalcitrant soil organic matter (Janssen et al., 2010), but increasing respiration in recently formed litter (Bragazza et al., 2006). The promotion of ecosystem respiration by N deposition was suggested to be potentially substantial due to increased decomposability of peat (Bragazza and Freeman, 2007; Bragazza et al., 2012). Part of such effects would be due to plant community shifts from N-conservative *Sphagnum* species to N-demanding vascular species. Such changes have been observed with long-term atmospheric N deposition (Aaby, 1994; Gunnarsson and Flodin, 2007; Greven, 1992) and experimental N addition (Heijmans et al., 2001; Larmola et al., 2013).

The interactions between plants and below-ground C cycling add complexity. Faster decomposition of vascular plant litter compared to *Sphagnum* litter (Lang et al., 2009) can offset enhanced C input to peat soils due to N fertilization. Also, the partitioning of the newly assimilated C into shoot compared to root tissue can be increased (Saarinen, 1998; Aerts et al., 1992) and the stem/leaf ratio may increase (Juutinen et al., 2010). As shoot and leaf litter generally decompose more rapidly than root and stem litter (Preston et al., 2000; Taylor et al., 1991), such structural change in plants can alter litter quality and in turn offset larger heterotrophic respiration (Neff et al., 2002).

An essential question for clarifying the effects of N deposition on C sequestration in peatlands is whether the changes in GEP and ER will compensate for each other. Short-term effects on the scale of years will likely differ from long-term effects on the scale of decades after ecosystem adaptation, for example, through shifts in relative abundances of different plant functional types (PFTs) and the effects of altered litter quality. Potential long-term decreases in C sequestration of peatlands owing to elevated N deposition from fossil fuel combustion would create an indirect positive feedback to greenhouse-gas-related climate warming.

To assess the outlined ecosystem and biogeochemical dynamics, we have recently presented the PEATBOG (Pollution, Precipitation and Temperature impacts on peatland Biodiversity and Biogeochemistry) model (Wu and Blodau, 2013), which is further outlined below. In this study, our objective was (1) to simulate the impact of varying N deposition on the C pools and fluxes of a northern bog; (2) to identify key parameters that determine the effect of N deposition on the C budget of ombrotrophic peatlands; (3) to identify long-term effects of N deposition on the C fluxes of such peatlands and (4) to identify empirical knowledge deficiencies that are important for long-term predictions.

1.1 Material and methods

1.1.1 Field experiment and empirical data for model evaluation

The environmental setting and model validation were provided by an N–P–K (hereafter NPK) fertilization experiment that was conducted at the Mer Bleue Bog (45°24′33.9″ N latitude, 75°31′7.35″ W longitude) located 10 km east of Ottawa, Ontario. The Mer Bleue Bog is a raised acidic ombrotrophic bog of 28 km² with peat depth ranging from 5 to 6 m at the centre to <0.3 m at the margin (Roulet et al., 2007). The vegetation coverage is dominated by mosses (e.g. *Sphagnum capillifolium*, *S. angustifolium*, *S. magellanicum* and *Polytrichum strictum*) and evergreen shrubs (e.g. *Rhododendron groenlandicum*, *Chamaedaphne calyculata*). Some deciduous shrubs (*Vaccinium myrtilloides*), sedges (*Eriophorum vaginatum*) and larch (*Larix laricina*) also appear in some areas (Moore et al., 2002; Bubier et al., 2006). The an-

nual mean air temperature is 5.8 °C, and the mean precipitation is 910 mm (1961–1990 average; Environment Canada). The coldest month is January (−10.8 °C) and the warmest month is July (20.8 °C) (Lafleur et al., 2003). Background N deposition at ca. 1.5 g N m^{−2} yr^{−1} is among the highest in Canada. Wet inorganic N deposition amounted to about 0.8 g m^{−2} yr^{−1}, and NO₃[−] contributed 60 % of this number (Moore et al., 2004).

The fertilization experiment was established in 2000–2001 (Bubier et al., 2007). Nitrogen was deposited as NH₄NO₃, and phosphorus and potassium (P, K) as KH₂PO₄ to triplicate 3 × 3 m plots, every 3 weeks from May to August. Experimentally enhanced N loads were equivalent to an annual deposition of 1.6, 3.2 and 6.4 g N m^{−2} yr^{−1} and the P and K load was equivalent to 5 and 6.3 g m^{−2} yr^{−1}, respectively. Therefore, the NPK ratios of the field treatments were higher in the treatments with higher N loads. As the N loads of 1.6, 3.2 and 6.4 g N m^{−2} yr^{−1} represented 5, 10 and 20 times the ambient wet summer N deposition at the Mer Bleue Bog, the field treatments are referred to as 5NPK, 10NPK and 20NPK in this study.

We validated our simulation model against measured data. The net ecosystem exchange of CO₂ (NEE) and ecosystem respiration (ER) were measured during the growing seasons 2001, 2003, 2005 and 2008 using a closed chamber technique. Gross ecosystem production (GEP) was estimated as the sum of NEE and the absolute value of ER (in figures ER shown with negative value). For the results and detailed methods see Bubier et al. (2007) and Juutinen et al. (2010). In short, ecosystem CO₂ exchange was measured weekly or every 2 weeks with about 2–3 min closure. The measurements were conducted when the photosynthetic photon flux density (PPFD) exceeded 1000 μmol m^{−2} s^{−1}, and in the dark using an opaque shroud. The measurements were repeated under full-, half-, quarter-light and dark conditions from May to August in 2001 and 2003, while CO₂ exchange was measured only under conditions of PPFD > 1000 μmol m^{−2} s^{−1} and dark in 2005 and 2008. In order to produce continuous flux time series for model evaluation of the CO₂ fluxes, the quadratic relationship between the observed GEP and photosynthetic active radiation (PAR) was derived for each replicate and each year in 2001 and 2003 and for each replicate of all the measured years in 2005 and 2008, due to the limited number of measurements in 2005 and 2008. The half-hourly PAR levels that were measured at the meteorological station were used to reconstruct half-hourly CO₂ exchange, which then was averaged over each day to obtain daily reconstructed GEP (referred as “observed” in this study). The observed and modelled daily GEP, ER and NEE fluxes were averaged for weekly periods and compared. To estimate C pools of the ecosystem, vegetation samples were collected twice, during the growing seasons of 2000 and 2008, and peat cores and soil water were sampled on three occasions from July to October in 2007 (Xing et al., 2010).

1.1.2 The PEATBOG model

The PEATBOG model has been developed for simulating the coupled C and N cycle in peatlands. It emphasizes material flow between the solid, water and gas phase of soil and the vegetation, a high spatial resolution of the soil compartment, stoichiometric control on C and N fluxes and a consistent conceptualization of C and N reactivity in vegetation and soil (Wu and Blodau, 2013). The model, version 1.1, is implemented in STELLA[®] and consists of four integrated sub-models. The environment sub-model generates daily WT depth from a modified mixed mire water and heat (MMWH) approach (Granberg et al., 1999), depth profiles of soil moisture, peat temperature and oxygen concentration; the vegetation sub-model simulates the C and N flows and the competition for light and nutrients among three PFTs: mosses, graminoids and shrubs. Competition among PFTs for both light and nutrients were exclusively modelled at the biogeochemical level. The soil organic matter sub-model uses a multi-pool approach for 20 soil layers to simulate dissolved and gaseous C and N at a fine scale. Finally, the dissolved C and N sub-model tracks the fate of C and N and closes the C and N budget.

Plant physiology is explicitly modelled following the Hurley pasture model (HPM), which contains functionally differed C and N pools in the plants (Thornley and Verberne, 1989; Thornley et al., 1995; Thornley, 1998). Major modifications were made to the HPM model to better represent the strong competition among peatland PFTs for light and nutrients (Appendix A4). Light competition was modelled using a multiple layer structure of the canopy and assuming an exclusive occupation of PFTs of the canopy layers. Beer’s law was applied to determine the descending light level from the high to low canopy following the sequence: graminoids > shrubs > mosses. The N uptake of PFTs was modelled by considering the interception of deposited N by mosses and the uptake of N by vascular roots. Mosses were assumed to take up 95 % of the deposited N unless P limitation occurs in mosses. When mosses are saturated with N at 20 mg N g^{−1} biomass, larger quantities of N enter the soil water and become available to vascular plants. The competition of the dissolved N among the vascular PFTs is conceptualized through the architecture of the roots and the uptake capacity of the three N sources (NH₄⁺, NO₃[−] and DON) that are modelled in each soil layer. Michaelis–Menten equations were used to quantify the N uptake from each soil layer and PFT. In the current version, the maximum uptake rate (V_{\max}) is larger and the half saturation constant (K_m) lower for NO₃[−] than for NH₄⁺, owing to the different uptake mechanisms (Kirk and Kronzucker, 2005). Shrubs and graminoids were not distinguished for their V_{\max} and K_m with respect to the N species. The uptake of N is then regulated by the concentration of N in the PFT, which in turn is determined by the N-use-efficiency and turnover of N pools in the PFT. The model is thus able to model the N uptake dynamically and avoids hard-coded differences be-

tween PFTs in terms of N dynamics. Light competition also interacts with the N competition through biomass growth and plant N content.

We previously evaluated the model against the empirically obtained soil moisture, temperature, daily and annual C and N fluxes from the eddy covariance tower and using multi-level piezometers and pore water peepers in the Mer Bleue Bog (Wu and Blodau, 2013). For the current analysis, some calibrated parameters were updated compared to PEATBOG 1.0 (Table 1), whereas model inputs remained the same, including geographic location and local slope of the site, daily precipitation and PAR, snow depth, annual average and range of air temperature, atmospheric CO₂, CH₄ and O₂ levels, annual N deposition level and the initial biomass of each PFT. In this study, the daily average precipitation, PAR and snow depth from 1999 to 2009 were derived from continuous (recorded at 30 min intervals) measurements from Fluxnet Canada (http://fluxnet.ornl.gov/site_list/Network/3). Gaps were filled by linear interpolation (less than 2 h) and otherwise by repeating the corresponding period of time from the closest available dates. The spin-up of the model was conducted to steady state for more than 10 000 years at a daily time step with repeated time series of all inputs. The results presented in this study are based on model version 1.1, unless stated otherwise.

1.1.3 Model input, strategy and evaluation

Model N input was from atmospheric N deposition at 1.5 g N m⁻² yr⁻¹ and N fertilizers. The modelled atmospheric N deposition incorporated wet and dry deposition and was composed of NH₄⁺ (30 %), NO₃⁻ (43 %) and DON (27 %). Fertilization with N in the model and field were identical at levels of 1.6, 3.2 and 6.4 g N m⁻² yr⁻¹, equally supplied as NH₄⁺ and NO₃⁻. Fertilizer was applied within 1 day in intervals of 21 days from 1 May to 31 August. Simulations were conducted with C:N interactions and without constraints posed by P or K availability in order to make the model output comparable with the NPK treatments in the field experiment. The P and K limitation on plants at the Mer Bleue Bog was alleviated in the experimental NPK fertilizer treatments, compared to the concurrent N-only treatments (Larmola et al., 2013; Wang et al., 2013; Wang and Moore, 2014). Therefore, despite the lack of a P or K component in the model, the modelling results are hereby referred to as “NPK” to be consistent with the NPK treatment in the field. The annual C and N fluxes between plant, soil and water were summed from the daily simulations to examine the trends of C and N cycling in the long-term.

The modelling strategy encompassed four steps. The first two steps simulated an 8-year period (here referred to as “short-term”) and steps three and four simulated an 80-year period (here referred to as “long-term”). First, we tested the performance of the PEATBOG 1.1 version at the Fluxnet Canada Mer Bleue site. To this end, short-term data from

control plots of the NPK fertilization experiments were employed. The initial state of the vegetation in 1999 was based on a vegetation cover as reported for the Mer Bleue Bog earlier (Moore et al., 2002). We used time series and goodness of fit that were quantified by the root mean square error (RMSE), linear regression coefficient (r^2) and the degree of agreement (d). The degree of agreement is in the index range from 0 to 1.0, with an index of 1.0 indicating perfect agreement (Willmott, 1982).

In the second step, the model was applied to the NPK fertilized treatments. We examined the deviations of C fluxes in model and empirical results and identified the external (e.g. difference in temperature inputs, differences between daily average values in model and empirical measurements under selected PPFD conditions) and internal (e.g. underestimation of biomass and leaf area index (LAI) of shrubs in the model) drivers of the deviations. As part of this procedure, it was tested whether these deviations could simultaneously be mitigated in all treatments by implementing correction factors relating to temperature and coverage of *Sphagnum* and the LAI of vascular plants. The simulated ER was scaled up for mid-day air temperature to be compatible to the observed ER that was generally obtained between 09:00 and 16:00 UTC–5 (Juutinen et al., 2010). The correction factor was obtained by calculating the corresponding ER at the maximum daily temperature based on linear relationship of air temperature to ER for each treatment. The correcting multipliers of ER were distinguished for each treatment to eliminate the effect of other factors, such as leaf area indexes and biomass, on the relationship between ER and T . The simulated daily GEP was scaled down by a specific factor for each fertilization simulation to generate the “best fit” to the observations. By investigating and minimizing discrepancies between initial simulations and observations, we identified the key parameters to be the relationship between photosynthetic capacities and N content (GEP_{max} – N) in PFTs that control the response of C cycling to N deposition. In the model, the total peat C pool was assumed to be constant in the upper 19 layers but variable in the 20th layer from 95 cm peat depth to the bottom of the peat column. This structure was meant to simplify the calculation of peat C sequestration in the bottom layer. In order to calculate the C stored in the upper 10 cm of the peat during the summer of 2007, we added the accumulated C inflow from plant litter to the C stored in peat on 1 June and then subtracted the C outflow for peat decomposition during the period from 1 June to 30 October.

In the next two steps, we explored how the long-term C fluxes were affected by N deposition. Furthermore the importance of the controls on the response of C cycling to N deposition that had been identified in the short-term simulations was investigated as well. In the third step, we simulated the effect of 80 years of N deposition at the fertilization levels of the field site and focused on the timescale of change in C pools and fluxes and its causes. In the fourth step, multiple long-term simulations were carried out by varying photo-

Table 1. Updated parameters in PEATBOG 1.1.

Name	Description	Value			Unit	Source
		Moss	Gram.	Shrub		
Plant						
$P_{max20,j}$	Photosynthetic capacity at 20°	0.0005	0.0022	0.002	$g\ CO_2\ m^{-2}\ s^{-1}$	1, 2
aPNUE	Slope of the photosynthesis rate–leaf N content curve	0.5	1	0.65	–	3
bPNUE	Intercept of the photosynthesis rate–leaf N content curve	0	–0.6	–0.3	–	3
$N_{amax,j}$	Maximum N content in leaf	1.5	2.5	2.5	$g\ N\ m^{-2}$	4
$K_{grow,sh,j}$	Shoot growth rate constant	0.033	0.095	0.012	day^{-1}	1, 5
$K_{grow,rt,j}$	Root growth rate constant	–	0.042	0.003	day^{-1}	1, 5
$K_{m,growC,j}$	Half saturation constant for substrate C in biomass growth	0.05	0.05	0.1	$g\ C\ g^{-1}$	6
$K_{m,growN,j}$	Half saturation constant for substrate N in biomass growth	5	0.3	0.5	$g\ N\ kg^{-1}$	6
$\rho_{C,j}$	Resistance parameter for shoot root transport of substrate C	–	60	50	$m^2\ day\ g^{-1}$	7
$k_{li,subsN}$	Constant of substrate N in litter	0.05	–	–	$g\ N\ g^{-1}$	8
$rR_{m,leaf,j}$	Leaf maintenance respiration rate constant	10	5	5	$g\ C\ kg\ C^{-1}\ day^{-1}$	9
$rR_{m,stem,j}$	Stem maintenance respiration rate constant	5	2.5	2.5	$g\ C\ kg\ C^{-1}\ day^{-1}$	9
$rR_{m,finert,j}$	Fine root maintenance respiration rate constant	2	–	–	$g\ C\ kg\ C^{-1}\ day^{-1}$	9
$density_{finert,j}$	Fine roots density	–	0.05	0.08	$g\ cm^{-3}$	10 Calibrated
$r_{mort,sh,j}$	Shoot mortality rate constant	0.005	0.0052	0.004	day^{-1}	11 Calibrated
$r_{mort,rt,j}$	Root mortality rate constant	–	0.0034	0.0009	day^{-1}	11 Calibrated
$r_{exuX,j}$	Exudation rate constant	0.005	0.001	0.001	day^{-1}	Assumed
SOM						
kC_{potq}	Inherent potential rate constant of decomposition	$kC_{potR} = 0.000015$ $kC_{potL} = 45\ kC_{potR}$			day^{-1}	Calibrated
k_{fix}	Base N_2 fixation rate	0.001			$g\ N\ m^{-2}\ day^{-1}$	12 Calibrated

M = C, N; q = labile, recalcitrant; Q = substrate, structural; X = shoots, roots, leaves, stems, fine roots, coarse roots; $DM_g = CO_2, CH_4, O_2$; $DM_s = NH_4^+, NO_3^-$, DOM; i = layer i ; j = plant functional type j . Values are assumed or calibrated based on these references: ¹ Chapin III and Shaver (1989), ² Small (1972), ³ Chapin III and Shaver (1989), ⁴ Bragazza et al. (2005), ⁵ Heijmans et al. (2008), ⁶ Thornley et al. (1995), ⁷ Reynolds and Thornley (1982), ⁸ Thornley and Cannell (1992), ⁹ Kimball et al. (1997), ¹⁰ Kirk and Kronzucker (2005), ¹¹ Moore et al. (2002), ¹² Moore et al. (2005).

synthetic response to nitrogen content in foliar tissue of the PFTs, as given by the key parameter GEP_{max-N} (modifications 1–3, Table S1 in the Supplement). By examining the trajectories of variables of interest in the long-term simulations, we evaluated the possible trends in C fluxes and pools towards the end of 21st century.

2 Results and discussion

2.1 Short-term effect of N deposition on C fluxes

We first compared the weekly averages of the simulated GEP, ER and NEE with the reconstructed values derived from observation during the summer in 2001, 2003, 2005 and 2008 (Fig. 1). The simulations captured the seasonal dynamics and 8-year trends of GEP, ER and NEE in control plots and under three N deposition levels. However, we found a bias towards overestimation of GEP and underestimation of ER and NEE (Fig. 1). The simulated GEP increased with N deposition level from 2.5–4.7 $\mu\text{mol C m}^{-2}\ \text{s}^{-1}$ in the control to 2.9–7.2 $\mu\text{mol C m}^{-2}\ \text{s}^{-1}$ in 20NPK. The model best predicted the effects of smaller N addition as Willmott's agreement (d) was highest in 5NPK and lowest in 20NPK (Table 2). The simulated GEP in 2001 was overestimated also in the control, which is likely a result of spinning up the model with the data set from the Fluxnet Canada tower site instead of the fertilization plots. The plots were located at a distance of approximately 100 m from the tower site, with which the model has been initialized for 39 % mosses, 7 % graminoids

and 54 % shrubs. The initial biomass and coverage of moss and graminoids on the fertilization plots were higher and of shrubs lower than at the tower site and in the model. Excluding the systematic overestimations in 2001, the coefficient of determination (r^2) of the simulated and observed GEP ranged from 0.70 to 0.77, and the RMSEs were between 0.69 and 1.59 $\mu\text{mol C m}^{-2}\ \text{s}^{-1}$ ($N = 43$). Larger discrepancies occurred at higher N levels.

Overall, the concurrent low degree of agreement (d) and high r^2 and RMSE between the simulated and observed GEP indicated a systematic bias in the simulations. The correcting factors were determined by establishing a linear slope between simulation output and the observations (Table 2). After applying the factors, the RMSE decreased to 0.34–0.40 $\mu\text{mol C m}^{-2}\ \text{s}^{-1}$ and the degree of agreement increased to 0.79 in the control and to 0.90 in the fertilization simulations (Fig. 2, Table 2). The model overestimated the LAI of mosses and underestimated the LAI of vascular plants in 10NPK and 20NPK (Table 3). The discrepancies in the simulated and observed moss cover and the vascular LAI together explained 86 % of the correcting factors. This outcome indicated a high importance of accuracy of plant composition and biomass when modelling C fluxes.

Simulated weekly average ER and NEE agreed more with the observations at the beginning of the fertilization and less so in 2008 (Fig. 1e–h). The RMSE of the simulated ER ranged from 2.26 $\mu\text{mol C m}^{-2}\ \text{s}^{-1}$ in 20NPK to 3.07 $\mu\text{mol C m}^{-2}\ \text{s}^{-1}$ in 5NPK, which was small compared to the standard deviation of the observation ranging from 2.5 to 5.4 $\mu\text{mol C m}^{-2}\ \text{s}^{-1}$. The overestimation of ER that in-

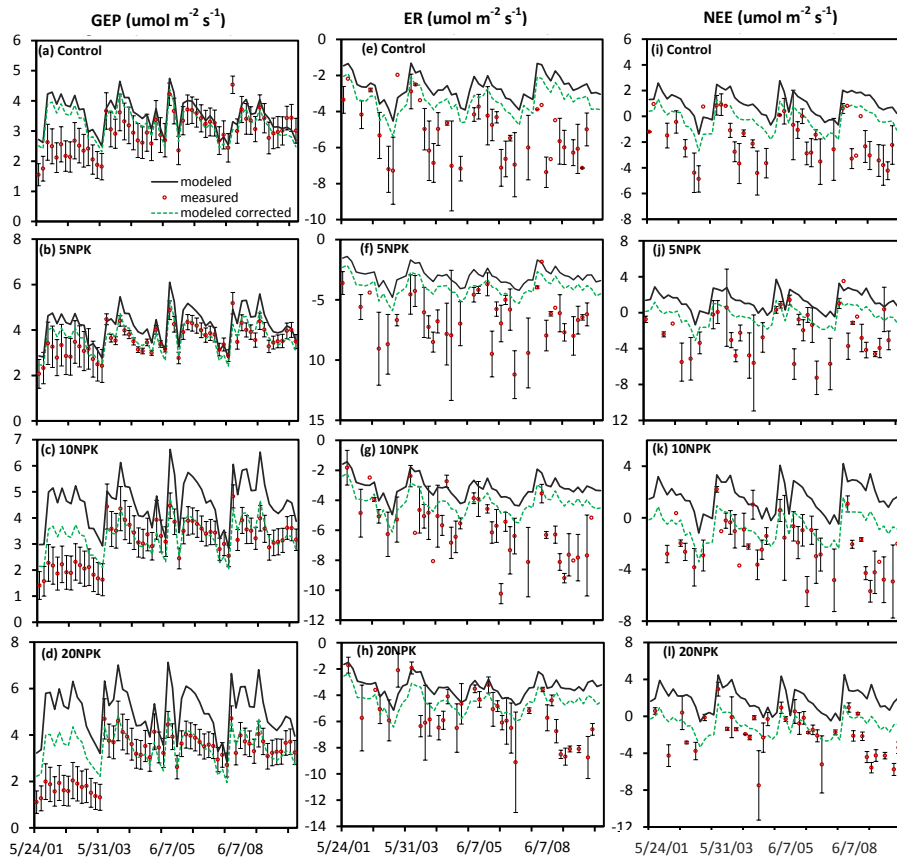


Figure 1. (a–d) Simulated and observed weekly average of gross ecosystem production (GEP), (e–h) ecosystem respiration (ER) and (i–l) net ecosystem exchange (NEE) May to Aug in 2001, 2003, 2005 and 2008. The green dotted lines represent weekly averaged CO_2 flux corrected for the biomass (a–d), for the air T–ER relationship (e–h), and NEE derived from the corrected GEP and ER. Positive NEE indicates that the simulated bog gains C. Note that P or K was not constrained in the model. The observed GEP was reconstructed from the observed PAR (half-hourly) and the derived GEP–PAR relationship based on the recorded GEP at full-, half-, quarter-light and dark conditions. The GEP–PAR relationship was calculated for each year and each treatment, with exceptions in 2005 and 2008 when only the full light measurements were available. A GEP–PAR equation was derived from all the available data between 2001 and 2008 to calculate the GEP in 2005 and 2008. The observed NEE was obtained from $\text{NEE} = \text{GEP} + \text{ER}$.

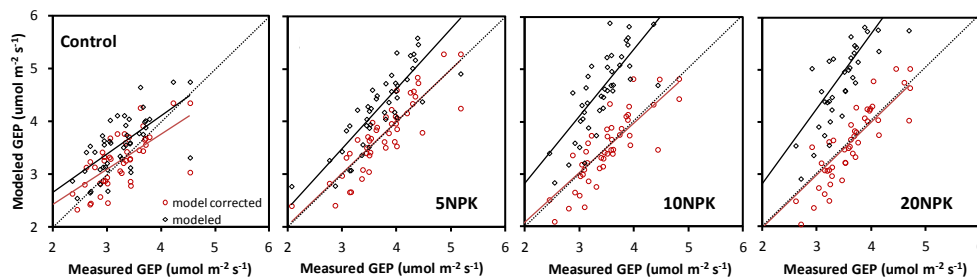


Figure 2. Observed versus simulated weekly average gross ecosystem production (GEP) in 2003, 2005 and 2008. The black circles and lines represent original simulation and the red circles and lines represent simulation adjusted by a factor producing the best fit (Table 2).

cluded respiration during nighttime was not surprising. Thus we corrected the simulated ER for temperature by using the slopes of the linear relationship between the daily average air temperature and ER in each simulation. The corrected ER and NEE agreed better with the observations. For

the ER in 5NPK, for example, the RMSE was reduced by $0.69 \mu\text{mol C m}^{-2} \text{s}^{-1}$ and the degree of agreement was raised by 0.2 (Table 2). The range of the corrected simulated ER was within the large deviation of the observed ER except for in 2008, when the observed respiration was larger than

Table 2. Regression statistics for the relationship between weekly averages of simulated and observed gross ecosystem production (GEP), ecosystem respiration (ER) and net ecosystem exchange (NEE) (unit: $\mu\text{mol m}^{-2} \text{s}^{-1}$) in the summer of 2001, 2003, 2005 and 2008. Both the observed and modelled GEP were calculated from the observed PAR (half-hourly) and the GEP–PAR relationship that were derived for each year and for each treatment. Exceptions were 2005 and 2008 when only the full light measurements were available. To calculate the observed GEP in 2005 and 2008, a GEP–PAR equation was derived from all the available data between 2001 and 2008. Observed NEE was obtained from $\text{NEE} = \text{GEP} + \text{ER}$.

GEP								
	Control		5NPK		10NPK		20NPK	
	Modelled	Model corrected	Modelled	Model corrected	Modelled	Model corrected	Modelled	Model corrected
Correcting multiplier	–	0.916	–	0.866	–	0.738	–	0.700
Slope b	0.72	0.66	1.14	0.99	1.28	0.94	1.44	1.01
Intercept a	1.21	1.11	0.06	0.05	0.27	0.20	0.07	0.05
r^2	0.50	0.50	0.76	0.76	0.70	0.70	0.77	0.77
RMSE (unit: $\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.52	0.40	0.69	0.34	1.33	0.37	1.59	0.36
Willmott's d	0.71	0.79	0.78	0.91	0.58	0.89	0.56	0.90
ER								
Slope b	0.30	0.31	0.24	0.25	0.19	0.18	0.17	0.16
Intercept a	–1.80	–1.18	–0.11	–2.24	–1.89	–2.95	–1.23	–0.87
r^2	0.40	0.37	0.53	0.48	0.32	0.25	0.24	0.18
RMSE (unit: $\mu\text{mol m}^{-2} \text{s}^{-1}$)	2.41	1.88	3.07	2.38	2.65	1.99	2.26	1.65
Willmott's d	0.49	0.47	0.44	0.65	0.49	0.71	0.83	0.81
NEE								
Slope b	0.72	0.66	1.14	0.99	1.28	0.94	1.44	1.01
Intercept a	1.21	1.11	0.06	0.05	0.27	0.20	0.07	0.05
r^2	0.50	0.50	0.76	0.76	0.70	0.70	0.77	0.77
RMSE (unit: $\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.52	0.40	0.69	0.34	1.33	0.37	1.59	0.36
Willmott's d	0.71	0.79	0.78	0.91	0.58	0.89	0.56	0.90

Table 3. Simulated and observed soil organic C pool (g C m^{-2}) in the upper 10 cm of peat, in mosses, plant stems, leaves and fine roots of treatments. Also, the leaf area index (LAI) of vascular plants and *Sphagnum* is displayed. The observed C pool was calculated from mass (Xing et al., 2010) assuming an average C content of 40 % in peat (Scanlon and Moore, 2000) and of 51% in plants (Aerts et al., 1992).

	Peat	Mosses	Vascular stems	Vascular leaves	Vascular fine roots	Vascular coarse roots	Vascular LAI	<i>Sphagnum</i> LAI*
Modelled								
Control	3463.3	77.5	82.7	50.3	59.7	219.0	1.0	1.9
5NPK	3517.5	106.0	117.2	70.5	67.2	231.6	1.5	2.4
10NPK	3562.3	76.2	170.1	101.8	75.7	242.5	2.3	1.6
20NPK	3611.9	28.9	254.1	152.8	83.7	244.8	3.2	0.5
Observed								
Control	680	31.0	190.2	190.2	45.9	245.8	1.9	1.1
5NPK	960	14.1	192.8	164.7	48.5	253.5	2.0	1
10NPK	1000	4.4	259.6	202.0	78.5	294.8	2.7	0.05
20NPK	1080	0.2	333.5	230.5	88.2	280.5	3.1	0
r^2	0.77	0.25	0.97	0.70	0.92	0.80		

* Values were estimated from the observed *Sphagnum* biomass and a specific leaf area of $0.02 \text{ m}^2 \text{ g}^{-1}$.

in other years also in the control (Fig. 1). This was likely due to variation of the site-specific conditions, such as the water table depth (WTD) and the vegetation cover. The measured summer average WTD from the eddy covariance tower site for model initialization was closer to the peat surface (–35 cm) in 2008 than in the other years. In contrast to the observations from the fertilization plots, ER was therefore

expected to be lower in 2008 than in the other years. This was even the case for the 20NPK plots, where a significant rise in WTD (–19 cm) was observed in the summer of 2008 (Juutinen et al., 2010). On the other hand, the simulated ER at mean WTD (–35 cm) was lower than the observed ER at mean WTD (–19 cm), suggesting that factors other than WTD might be stronger regulators of ER. Indeed, ER was

found to be the most related to factors indicating more vascular biomass and less *Sphagnum* biomass, whereas the correlation between ER and WTD was only 0.28 (Juutinen et al., 2010). The model underestimated the vascular and overestimated the *Sphagnum* biomass in 2008 (Table 3). Both deviations likely contributed to the underestimation of ER.

2.2 Short-term effect of N deposition on C pools

Simulated C content in biomass generally increased in shrubs and grasses with increasing N input but not in mosses. The carbon in moss biomass increased only in the 5NPK simulation and declined in the 10NPK and 20NPK simulations (Table 3, Fig. 3). The simulated moss coverage declined more slowly than in the observations (NPK treatments) and was only impaired from 2005 on, when it had nearly disappeared in the 20NPK treatment in the experiment (Juutinen et al., 2010). This may be caused by the fact that we simulated impacts of N, while the experiments have shown that the impact of the NPK treatment is stronger, i.e. shrub growth is enhanced more strongly, than that of the N-only treatment (Larmola et al., 2013). The initial overestimate of moss biomass and surface cover and underestimate of shrub biomass compared to on-site observations likely contributed to the delay in moss disappearance (Table 3). The simulated aboveground biomass C of vascular plants increased with N load, following the sequence of control < 5NPK < 10NPK < 20NPK. In stems and leaves, biomass C increased from 83 and 50 g C m⁻² in the control to 254 g C m⁻² and 153 g C m⁻² in 20NPK. In comparison, the belowground biomass was less affected by N deposition, especially with respect to coarse roots that increased the most in the 20NPK simulation at 12 % (Table 3). Both the simulated leaves and stems of vascular plants tripled in the 20NPK simulations compared to control simulation at the end of the 8-year simulation in 2007 (Table 3). The model uses fixed leaf/stem ratios of vascular plants and does not take into account the observed larger biomass increases in stems than in leaves (Juutinen et al., 2010). This likely added to the overestimation of production of mosses and underestimation of negative effects of vascular plants on *Sphagnum* mosses (see also Chong et al., 2012).

The simulated peat C pool was larger than the observation mainly due to a higher bulk density in the model than observed in the control and treatment plots, where the average bulk density of the upper 10 cm peat was 0.017 g cm⁻³ in the control plot and increased to between 0.024 g cm⁻³ and 0.026 g cm⁻³ in treatment plots (Bubier et al., 2007). In comparison, the bulk density in the model was stable for each peat layer and was averaged from an earlier measurement at the site, which ranged from 0.01 to 0.05 g cm⁻³ in the upper 10 cm of peat (Blodau and Moore, 2002). The simulated peat C pool did not show the abrupt temporal changes that characterized the plant C pool, but a steady trend of increases with raised N input. The greatest increase occurred in

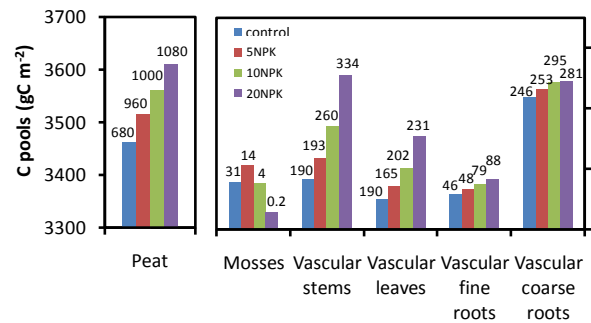


Figure 3. The simulated (bars) and observed (values) summer C pools in plants and peat after 8 years of fertilization. Observed data from Xing et al. (2010) are shown in Table 1.

20NPK at 149 g C m⁻² in the soil organic mass after 8 years of fertilization. As the model considers litter as peat, the simulated increase in the C pool in the peat was in line with the large increase in the litter accumulation, up to 10 fold up to 410 g C m⁻² in the 20NPK plots compared to 49 g C m⁻² in the control plot (Bubier et al., 2007). Even though our model underestimated C in moss biomass C in response to N input, the simulated relative change in carbon content in the peat and vascular plant biomass highly agreed with the observations, with coefficients of determination (r^2) ranging from 0.70 to 0.97 ($N = 4$) (Table 3).

Overall, an accurate estimation of plant composition and leaf biomass with the fertilization level and length was a prerequisite for a correct C flux model output of the PEATBOG model. In this study we cannot expect perfect agreement between model and observed data because P or K addition was not included in the model. The importance of plant coverage for C fluxes was empirically evident at the Mer Bleue Bog, where the graminoid-dominated (mainly *Carex* spp.) areas were found to have larger net ecosystem production than the shrub-dominated areas during a dry summer in 2001 (Bubier et al., 2003). Similarly, short-term C fluxes were influenced by PFT distribution in a plant removal experiment in an ombrotrophic bog in the UK (Ward et al., 2009). Differences in green biomass of the dominant PFTs also explained the differences in growing season NEE between peatland sites (Laine et al., 2012). The acceleration of C cycling in our simulations with growing graminoid abundance are in line with reports of significantly higher summer production and NEE in wetter peatlands containing more sedges than the Mer Bleue Bog (Laine et al., 2012). The relative dryness of the Mer Bleue Bog may thus be a reason for a continued lack of sedge vegetation in the investigated fertilization plots that was not predicted by the model. When predicting effects of changes in nutrient availability on vegetation dynamics, differences and changes in water table position need to be accounted for.

2.3 Long-term effects of N deposition on C pools

Overall, the model predicted the Mer Bleue Bog to become a larger C sink when exposed to long-term N deposition at the rate of $6.4 \text{ g N m}^{-2} \text{ yr}^{-1}$ (Fig. 4). Most C was stored in peat rather than in plants that maintained a similar C pool of 911 to 1045 g C m^{-2} in 2080, regardless of simulated N treatment, after steady state was attained (Fig. 4a). The allocation of C among PFTs and their parts was substantially altered, though. After an initial surge, the C pool in mosses declined from the fourth year on in 20NPK and from the sixth year on in 5NPK (Fig. 4b). It re-stabilized in 5NPK and 10NPK at equally higher levels than in the control after 20 years of fertilization. In the simulated 20NPK treatment moss continuously declined to extinction after 15 years of fertilization (C pool in mosses $< 1 \text{ g m}^{-2}$). Carbon in both the shoots and roots of graminoids expanded concurrently to the decline of C in mosses, following the sequence of control $< 5\text{NPK} < 10\text{NPK} < 20\text{NPK}$ (Fig. 4c, d). From a small contribution of 7% (shoots) and 4% (roots) of C in the plants, graminoids became the dominant PFT and ultimately stored most C in the simulated 10NPK and 20NPK treatments. However, the increase of C in the shrub shoots and roots was sustained only during the first 5 years and decreased by approximately 25–90% in 5NPK to 20NPK in roots (Fig. 4e, f) after 80 years of fertilization. This finding does not consider larger growth increases in deciduous shrubs compared to evergreen shrubs that were reported in field investigations (Larmola et al., 2013). At the Mer Bleue fertilization experiment, graminoids are scarce and only some scattered *E. vaginatum* occur. However, the ferns *Dryopteris*, *Cystopteris* and *Thelypteris* were established and contributed up to 24% to the abundance of vascular plant leaves in the 20NPK plots after 11 years of fertilization (Larmola et al., 2013).

As most of GEP was eventually stored in peat, the average C sequestration rate increased from $8 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the control to 78, 150 and $181 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 5NPK, 10NPK, and 20NPK after 80 years, resulting in 4, 7, and 8 cm of additional vertical peat growth (Fig. 4g). Along with an increase in C sequestration, the labile C content of peat increased substantially once graminoids dominated the litter source. In addition, the C/N ratio of peat in the upper 40 cm widened in the 5NPK and 10NPK simulations and at the beginning in the 20NPK simulation as well (Fig. 4n). The increasing C/N ratio in the 5NPK, 10NPK and at the beginning of the 20NPK was a result of a faster net sequestration of C than N in the peat. The limited N sequestration in the peat subject to low N inputs was attributed to the living moss layer that effectively retained most of the N at the ground surface (Fig. 4b). When mosses were saturated and eliminated from the vegetation community, N filtration failed and the N that had previously been retained by the mosses was transferred into the peat N pool. Ratios of C/N ratio in the peat thus began to decrease after 30 years in the 20NPK treatment (Fig. 4i).

2.4 Long-term effects of N deposition on C fluxes

Annual average GEP, ER and NEE were raised by the addition of N, and severe changes occurred only during the first 10 years of fertilization before new stable states were attained (Fig. 5). After 80 years, annual average GEP increased by 25, 44 and 43%, and annual ER by 12, 20 and 21% in the simulated 5NPK, 10NPK, and 20NPK treatments, respectively. The model simulated great increases in GEP that were mainly attributed to the expansion of graminoids that were more productive than mosses and shrubs in the model, such as also observed in field measurements (e.g. Laine et al., 2012).

Ecosystem respiration consists of two decoupled C fluxes, autotrophic respiration (AR) and heterotrophic respiration (HR). In our model, autotrophic respiration was limited by the level of plant biomass, which showed little sensitivity to the N deposition levels at the final states (Fig. 4a). This interpretation is supported by a strong correlation between plant biomass and AR. For example, lower ER was found in the 20NPK fertilization plots than in others in 2005, when the increase in the biomass of vascular plants had not yet compensated for the loss of *Sphagnum* biomass (Juutinen et al., 2010). Evidence of a moderate AR response to N was found in *Eriophorum vaginatum* after 5 years of N fertilization at $5.6 \text{ g N m}^{-2} \text{ yr}^{-1}$ in a Scottish ombrotrophic bog (Currey et al., 2011). In the long-term, subtle changes in AR is expected at the fertilization plots in the Mer Bleue Bog, taking into account the limit to biomass build-up at the steady state and moderate responses of consumption of photosynthetically assimilated C through AR.

In contrast, the effects of N deposition on HR showed a significant delay for approximately 10 years in all simulated treatments. The simulated delay was in line with the 9-year period before the initial significant increase of ER was observed in the 20NPK treatment plots (Larmola et al., 2013). The lagged responses of HR to N deposition corresponded to the expansion of vascular plants and increased litter production (Juutinen et al., 2010, Fig. 4). After the first 10 years, HR accelerated in the order control $< 5\text{NPK} < 10\text{NPK} < 20\text{NPK}$, and peaked at 43% above the level of the controls in 20NPK after 80 years (Fig. 6c). The simulated increase in HR in 20NPK was significant already after the first 40 years of simulation ($r^2 = 0.3$, $N = 40$, $p < 0.001$). This trend is in line with speculation that the decomposability of the fresh litter from the vascular plants had increased in the experiments (Juutinen et al., 2010).

The simulated annual HR was averaged for every 11 years, which was the length of the repeated climatic input, to eliminate the effects of short-term environmental factors. HR was, under these conditions, highly correlated with the fraction of labile C ($r^2 = 0.97$, $p < 0.001$, $N = 36$) (Fig. 7a). Recent reports have emphasized the role of intrinsic peat decomposability in regulating HR. The increase of the HR coincided with declining lignin, polyphenol and acid unhydrolyz-

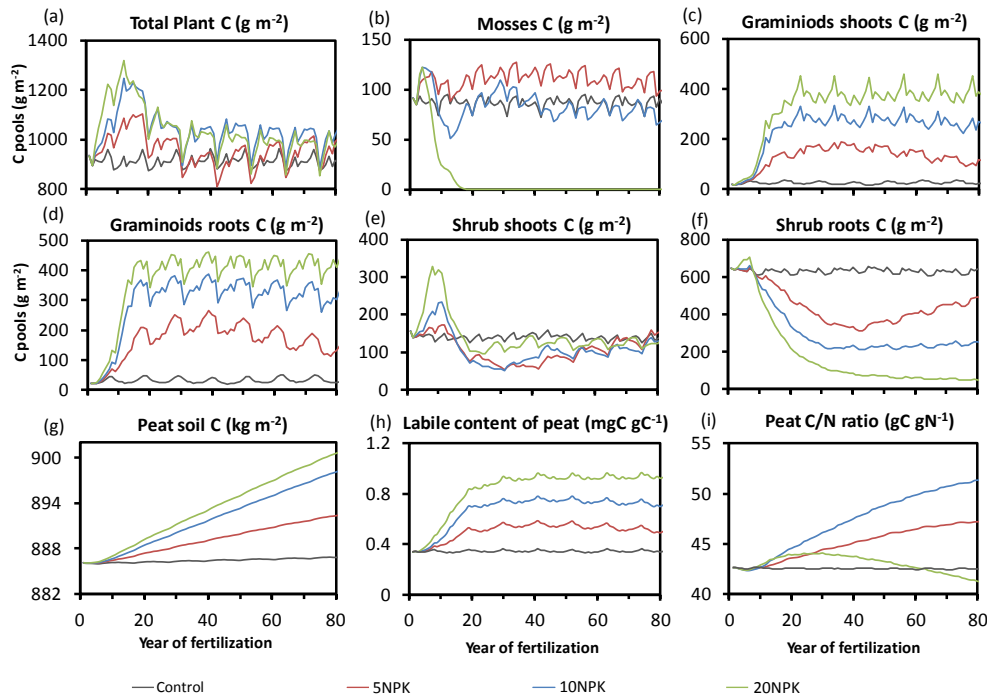


Figure 4. (a–i) Simulated annual average C pools in plants and peat, labile fraction of peat (mg C gC^{-1}) and C/N ratio in the upper 40 cm of peat over 80 years of fertilization. Short-term variation is due to variation in the climatic driver.

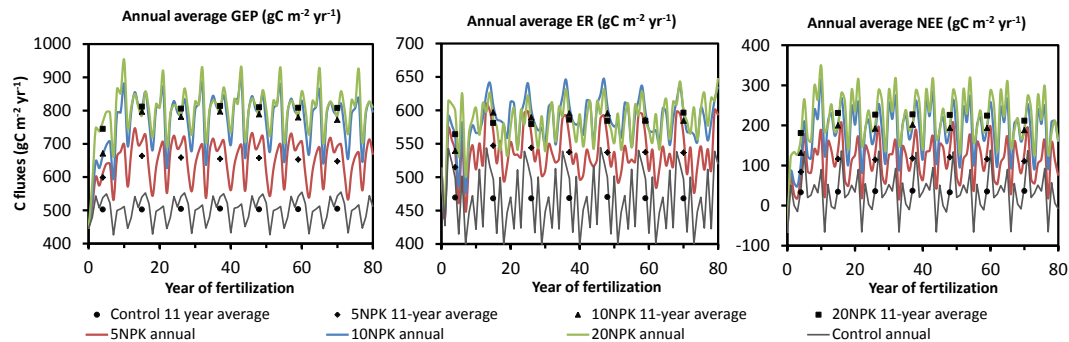


Figure 5. Annual average gross ecosystem production (GEP), ecosystem respiration (ER) and net ecosystem exchange (NEE) over 80 years of fertilization. Positive NEE indicates C gain into the bog.

able residue content in peat, as has been found both in N fertilization experiments (Aerts et al., 2006; Limpens and Berendse, 2003; Breeuwer et al., 2008) and along gradients of chronic N deposition (Bragazza et al., 2006; Bragazza and Freeman, 2007; Bragazza et al., 2009). In addition to the fresh litter, more active root exudation can also produce highly biodegradable substrates to trigger additional microbial respiration in NPK fertilized peat (Larmola et al., 2013). Changes in the peat hydraulic conditions may also change the peat quality and decomposability and have been observed on the 20NPK plots after a decade of fertilization (Larmola et al., 2013). Evidence of increases in HR following an increase in peat decomposability has been found also in pristine peat-

lands, where N fertilization altered the peat quality towards more labile and enhanced HR (Bragazza et al., 2012). Moreover, stimulation of peat decomposability due to N fertilization has been suggested also in Arctic tundra (Mack et al., 2004). On the other hand, the modelling results here also suggest a maximum level of HR that would be approached when the system has established a new stable state with little change in either litter production or vegetation composition (Fig. 4a–f, Fig. 6a).

The correlation between simulated HR and the C/N ratio of peat was poor when all data were included ($r^2 = 0.07$, $N = 36$) (Fig. 7b) and only somewhat improved when excluding the first 33 years with strongly varying litter in-

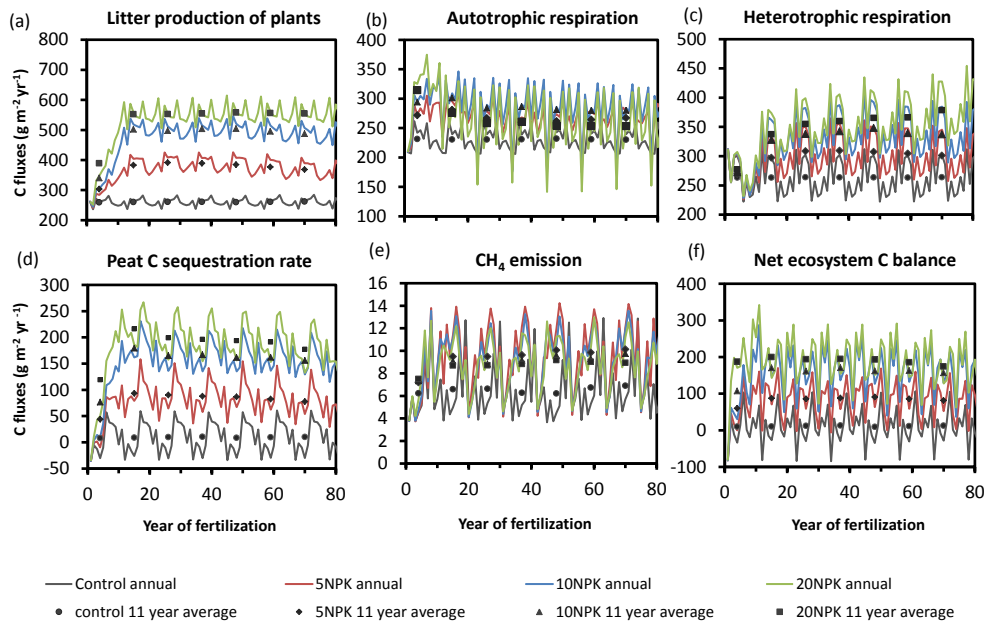


Figure 6. Simulated annual average C cycling rates over 80 years of fertilization.

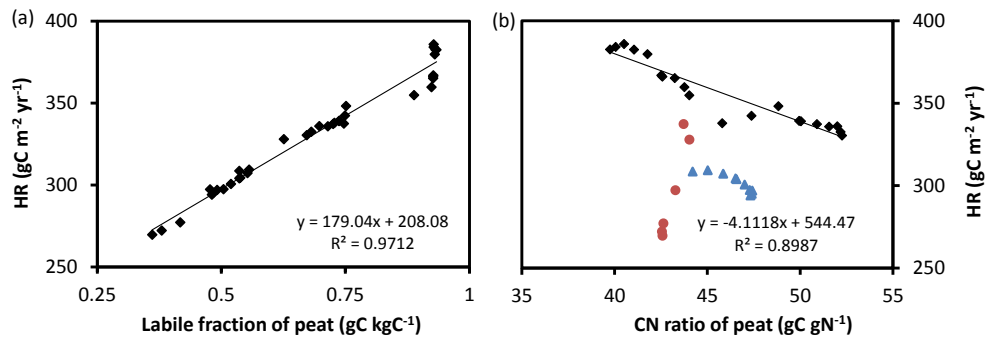


Figure 7. (a) The relationship between modelled annual heterotrophic respiration in the 20NPK treatment (HR) and labile fraction of peat C and (b) between HR and C : N ratio above 40 cm of peat (g C g N^{-1}). The values were averaged for each 11-year interval with repeated environmental drivers; black diamonds are values from 2021 to 2130 in 10NPK and 20NPK, red circles are from 2021 to 2130 in 5NPK and blue triangles are from 1999 to 2020 in 5NPK, 10NPK and 20NPK.

put to the soil ($r^2 = 0.31$, $N = 30$). The relationship was on the other hand much stronger and highly significant when disregarding values from the 5NPK simulation ($r^2 = 0.90$, $p < 0.001$, $N = 20$) (Fig. 7b). The outlier of 5NPK in the regression of HR and C/N ratio revealed a non-linear change in the N retention of the peat corresponding to the vegetation shift from shrub-*Sphagnum* dominated to graminoid dominated. The conservative decomposition of *Sphagnum* litter led to a low and narrow range of C/N ratio in the peat from 42 to 46 (Fig. 7b) due to more retention of N per C, as was suggested by Bragazza et al. (2009). Following the change in litter type from *Sphagnum* to vascular in 10NPK ($r^2 = 0.90$, $N = 12$), more N per C was released from decomposition and the C/N ratio of peat increased (Fig. 4i). In the only simulation where mosses were diminished in the system, 20NPK,

the increase of C/N ratio in peat ceased and even reversed following the establishment of grasses as predominant PFT ($r^2 = 0.89$, $p \ll 001$, $N = 10$) (Fig. 4i). This reversal reflects the direct N input from deposition without the “moss filter” (Fig. 4b). Meanwhile, the strong inverse correlation between HR and C/N ratio holds true in the vascular-dominated systems (10NPK and 20NPK) ($r^2 = 0.99$, $N = 12$), suggesting a potential increase of HR with the diminishing C/N ratio if the high N deposition sustained beyond the simulation period (Fig. 4i).

In the simulations GEP increased more strongly than ER, which resulted in a large increase of NEE from $45 \text{ g C m}^{-2} \text{ yr}^{-1}$ to 122, 188 and $178 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 5NPK, 10NPK and 20NPK, respectively, and after 80 years of simulation. Towards the end of this period, NEE in 10NPK and

20NPK simulations converged and were substantially higher than the NEE in 5NPK simulations (Fig. 5c). Promoted by the enhanced GEP, the aboveground litter input increased substantially from 261 to 555 g C m⁻² yr⁻¹ in 20NPK in 2080 (Fig. 6a). Together with the slow increase in ER, annual C sequestration was raised by a factor of 2–4 (Fig. 6d). A large increase of C sequestration has not been observed in the fertilization experiment that has to date sustained a vegetation community dominated by shrubs (see Juutinen et al., 2010; Larmola et al., 2013). Accordingly, modified simulations with predominance of shrubs and mosses led to much smaller C sequestration rates (see Sect. 3.6). The deviation between modelled and observed C sequestration rates in the first decade of the experiment thus hinges on the difference in the predominant PFT between model and reality. Regarding belowground heterotrophic processes, some other noteworthy effects occurred. The simulated CH₄ fluxes also increased in all fertilized treatments by a factor of 2–3 up to 14 g C m⁻² yr⁻¹. This outcome was mostly an effect of the more effective transport of CH₄ by the expanded roots of graminoids (Fig. 6e). The increased ratio was analogous to the observed 2- to 4-fold difference between the growing season daily CH₄ emission rates in the graminoid-dominated collars and the shrub-dominated collars during 2004 to 2008 in the Mer Bleue Bog (Moore et al., 2011). Carbon loss as dissolved organic and inorganic C changed little through N deposition (not shown).

The simulated net ecosystem C balance (NECB) that was obtained by subtracting the loss of DOC and CH₄ from NEE increased greatly from 20 g C m⁻² yr⁻¹ to 87, 150 and 138 g C m⁻² yr⁻¹ in 5, 10 and 20NPK respectively after 80 years of simulation. The simulated C sequestration was above the reported long-term range in boreal peatlands of 16 to 23 g C m⁻² yr⁻¹ (e.g. Turunen et al., 2004), and similar to the reported values for short-grass steppe and wet tundra of 117 and 141 g m⁻² yr⁻¹ (Knapp and Smith, 2001). It is noteworthy that the N deposition level used in this study was much higher than under natural conditions and predicted future N deposition levels up to 2 g N m⁻² yr⁻¹. Such high C sequestration rates, however, may not be sustained over even longer periods given the potential increase of HR in our simulation. Corresponding to the decrease in C/N ratio as discussed above, a linear decreasing of NECB was clear and C loss was predicted for 20NPK simulation: the slope of 0.28 g C m⁻² yr⁻¹ of the NECB simulation resulted in a net C uptake of zero after about 700 years of N fertilization (Fig. S2 in the Supplement). The slow response in the C sequestration of the peatland to N deposition was similar to the slow response of peatlands to climatic disturbances predicted by the HPM model, in which 500–600 years were needed for the peatland to cease C sequestration (Turetsky et al., 2012). The results from the HPM model suggested the importance of mosses for maintaining the cool environment and for buffering water table variations upon changes in pre-

cipitation. In this study, mosses were also essential for peat to sustain a high C/N.

2.5 Mechanisms underlying simulated effects of N deposition on GEP and NEE

In the model, GEP in vascular plants increased at all N deposition levels and in mosses below fertilization of 3.2 g N m⁻² yr⁻¹. The model overestimated GEP in the 10NPK and 20NPK simulations compared to observations during the first 8 years owing to a greater increase in the graminoid biomass and the higher photosynthetic capacity (GEP_{max}) of graminoids and shrubs than of mosses. In the current model version, GEP_{max} was positively and linearly related to the N content below the maximum N content in the shoots of plants (2.5 g N m⁻²) and slopes followed the sequence: shrubs < mosses < graminoids (Fig. 8a, Appendix A). The GEP_{max} of mosses was negatively related to leaf N content and those of graminoids and shrubs were not affected when leaf N exceeded the maximum N content (Fig. 8a). The sequence of slopes and the shape of the GEP_{max}–N content relationship was based on observations across growth forms and N gradients.

Specifically, the photosynthetic capacity in *Sphagnum* mosses was found to increase with N content in tissue with species-specific yields and without increases in production (Granath et al., 2009a, b; Granath et al., 2012). The optimal N content for GEP_{max} was suggested to occur at approximately 12.9 mg N g⁻¹ and for photosynthetic N-use efficiency at 9.1 mg N g⁻² in *Sphagnum balticum*, but not in the other two *Sphagnum* species (*S. fallax* and *S. fuscum*) (Granath et al., 2009b, 2012). The foliar N content and GEP_{max} have usually been found to be positively and linearly related in grasses (e.g. Garnier et al., 1999; Chen et al., 2005) and shrubs (e.g. Wright et al., 2001). Across growth forms, species with larger specific leaf area tend to have higher GEP_{max}–N content slopes than species with smaller specific leaf areas, such as shrubs (Reich et al., 1998). The above arguments support a positive GEP_{max}–N content relationship. In such a relationship, an increase in N availability raises the investment in photosynthetic N use in vascular plants (Hikosaka, 2004) and in *Sphagnum* mosses with low N content (Granath et al., 2009a).

In contrast, in long-term N fertilization experiments (8- to 15-year N amendments) a decoupling of GEP_{max} and foliar N has been observed in a red pine forest (Bauer et al., 2004), and more importantly in the ericaceous shrubs at the Mer Bleue Bog (Bubier et al., 2011). Bubier et al. (2011) argued that these long-lived shrubs have adapted to a low-N environment and they allocate N to growth, yet with no changes in the photosynthetic rates. This finding was in line with the reported maintenance of metabolic homeostasis in *Carex* and *Eriophorum* under increased nutrient availability in Arctic tundra (Shaver and Laundre, 1997). Similarly, photosynthesis of *Calluna* was found to be unaffected by experimentally

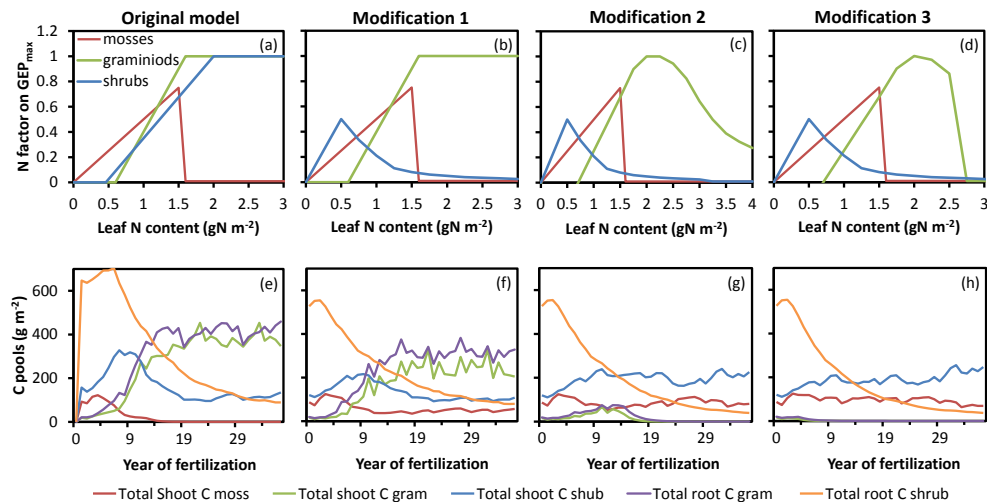


Figure 8. (a–d) The dependency of photosynthetic capacity (GEP_{max}) on leaf N content in simulations (original and modifications 1–3) and (e–h) consequent C pools in PFTs during 40 years of fertilization at $6.4 \text{ g N m}^{-2} \text{ yr}^{-1}$. (a) Original model with a positive relationship between the photosynthetic capacity (GEP_{max}) and N content in vascular PFTs, (b) modification 1 with a negative GEP_{max} –N relationship in shrubs only, (c, d) modification 2 and 3 with negative GEP_{max} –N relationship when leaf N content exceeds 1.5 g N m^{-2} (equivalent to $0.03 \text{ g N g C}^{-1}$) in shrubs and exceeds 2 g N m^{-2} (equivalent to $0.024 \text{ g N g C}^{-1}$) in graminoids.

added N (Whitehead et al., 1997; Currey et al., 2011). This finding was attributed to the slow growth rates and N use priorities of *Calluna*. Although a large increase in graminoid biomass was not found after 9 years of fertilization in the NPK plots of the Mer Bleue Bog, the observed limitation of GEP_{max} to benefit from high N content in shrubs indicated a lesser competitive advantage of shrubs compared to other PFTs, including graminoids (Bubier et al., 2011).

To examine the importance of such empirical findings, we modified the GEP_{max} –N relationship of shrubs (Fig. 8b, Appendices A and B, modification 1) according to the observed lack of relationship within the leaf N content range of 1.5 and 2.5 g m^{-2} (Bubier et al., 2011), equivalent to 0.03 to $0.05 \text{ g N g C}^{-1}$ in the model. None of the modifications improved model performance in all aspects. Modification 1 resulted in a better fit of the modelled GEP during the first 5 years of fertilization in 20NPK (Fig. 8a). On the other hand, mosses did not decline as much in the long-term simulation as they did in the fertilization plots (Fig. 8f). This effect was due to less shading from vascular plants in the model. Alternatively, modifying both the GEP_{max} –N relationship of shrubs and graminoids (modification 2, 3) (Fig. 8c, d) greatly reduced the discrepancies between the simulated and observed GEP and NEE (Fig. 9a). Also, in these modifications, mosses did not decline, but graminoids did not increase either, as was also observed with respect to the graminoids in the field. In both modification 2 and 3, the GEP_{max} of graminoids decreases with leaf N content above 2 g N m^{-2} , equivalent to $0.024 \text{ g N g C}^{-1}$ (Fig. 8c, d). The biggest improvement of model performance regarding C fluxes occurred with modification 3, in which GEP_{max} in

both graminoids and shrubs strongly decrease with N content in shoots above their optimal N contents (Fig. 8d). This modification was not realistic if we compare it with the observations, i.e. a lack of clear trend in the leaf photosynthetic capacity with leaf N content, more deciduous shrub biomass in the NPK fertilized plots (Bubier et al., 2011) and a different type of vegetation in the model and in the experimental area. However, it shows that the original model with its positive GEP_{max} –N relationship in shrubs was not able to capture the observed type of ecosystem trajectory.

The improvement in simulations with non-linear dependency of GEP_{max} to N content suggested that the relationship between GEP_{max} and N in all PFTs follows a unimodal model. This interpretation includes the graminoids, which were earlier characterized by a linear dependency of GEP_{max} on N content (Sage and Pearcy, 1987; Garnier et al., 1999). Although there have been reports of a threshold N content for photosynthesis in graminoids, growth of a graminoid (*Eriophorum vaginatum*) was not affected, while photosynthesis accelerated after 5 years of N amendment at $5.6 \text{ g N m}^{-2} \text{ yr}^{-1}$ (Currey et al., 2011). Similarly, graminoids were found maintaining their metabolic homeostasis while accumulating more biomass after 2 years of fertilization at $10 \text{ g N m}^{-2} \text{ yr}^{-1}$ and $5 \text{ g P m}^{-2} \text{ yr}^{-1}$ in an Arctic tundra (Shaver and Laundre, 1997). Currey et al. (2011) suggested that additional investment in root growth or storage of the assimilated C contributed to the decoupling of aboveground growth and photosynthesis (Currey et al., 2011). Our results support this argument as increases in the root/shoot growth ratio and photosynthesis rate were simulated, if only during the first 3 years (Fig. S1a in the Supplement). Using mod-

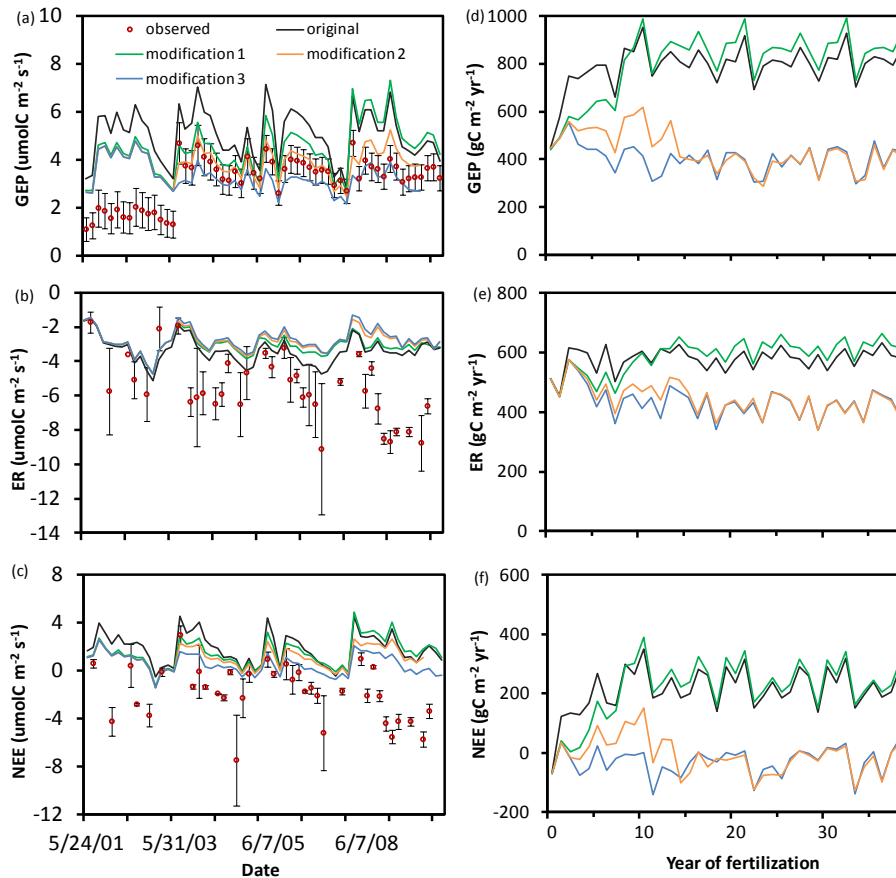


Figure 9. (a–e) weekly averages of simulated and observed gross ecosystem production (GEP), ecosystem respiration (ER) and ecosystem exchange (NEE) from May to August 2001, 2003, 2005 and 2008 fertilized with $6.4 \text{ g N m}^{-2} \text{ yr}^{-1}$. (d–f) Annual GEP simulations (1–3) representing the same parameterizations as in Fig. 8b–d.

ification 3, increases in the growth in graminoid roots and GEP were not sustained due to the limited photosynthesis (Fig. S1b in the Supplement), and ultimately led to a complete decline of graminoids (Fig. 8h). Indeed, increases in the biomass of graminoids have not been observed at the N fertilization plots of the Mer Bleue Bog to date. *Eriophorum vaginatum* is a common graminoid at Mer Bleue, but it is more abundant in the moister areas of the bog and scarce at the location of the fertilization experiment, where only scattered individuals occur. The GEP_{max} of graminoids in the fertilization plots would need to be further examined in order to certify whether an N content threshold exists for photosynthetic capacity in graminoids. In addition, other feedbacks may have affected the plant competition and should be considered to improve model predictions. For example, the recently observed increase in the water table level in 20NPK may facilitate the expansion of graminoids in the future (Larmola et al., 2013), while the increase of the water table level was negligible in the current model.

2.6 The importance of timescale for the effect of N deposition on C fluxes

The simulated annual GEP, ER and NEE showed large variations among the varied $\text{GEP}_{\text{max}}\text{--N}$ relationship in the first years and separated into two groups after 20 years of fertilization (Fig. 9d–f). The results showed a continuing positive effect of long-term N deposition on the NEE of the graminoid-dominated system, whereas a release of C from the peatland occurred in the shrub–moss-dominated scenarios. The changes in the C fluxes in the first few years were not indicative of the long-term changes in C fluxes, which started to emerge after 10 years. The original simulation and the modification 1 simulation predicted a shift of the PFTs from shrub–moss-dominated to graminoid-dominated. This path turned the bog into a large C sink after 20 years of fertilization in the simulated 20NPK treatment at a deposition of $6.4 \text{ g N m}^{-2} \text{ yr}^{-1}$. In contrast, in simulations with modifications 2 and 3 the bog remained shrub–moss-dominated and switched to a small C source after 20 years of fertilization in the same treatment (Fig. 9d–f). In the graminoid-dominated

scenarios, the peatland contained a much higher total above-ground biomass, and had a significantly higher GEP, ER and NEE than in the shrub–moss-dominated type.

Previous work has also suggested occurrence of alternative stable states in peatlands. Using an analytical modelling approach, Hilbert et al. (2000) identified two stable ecological states of peatlands, resembling either wet fens with thinner peat and dry bogs with thicker peat. In contrast to these states, our simulation suggested a higher productivity and peat accumulation in the graminoid-dominated than the shrub-dominated system. A promotion of plant productivity by N deposition, within their tolerance range, was not considered by the Hilbert et al. (2000) model, which simulated a limited primary production in fens. A dichotomy in vegetation community composition was also predicted by an N-sensitive vascular–*Sphagnum* competition model (Pastor et al., 2002). The authors showed a strong dependence of the equilibrium size of plants regarding their competition for nutrients, as was also the case in our simulations (Figs. 8–9).

On the ecosystem scale, other processes beyond those simulated need to be considered. For example, further PFTs, in particular trees, herbs or deciduous shrubs, might benefit from N enrichment and become important in the competition among plants for resources (Tomassen et al., 2003; Huotari et al., 2008). Accordingly ferns and birch have become more prevalent at the $6.4 \text{ g N m}^{-2} \text{ yr}^{-1}$ (PK) fertilization level in the Mer Bleue bog (Larmola et al., 2013; personal observation). Moreover, competition among species within a PFT could either reinforce or abate the competitive differences among PFTs through replacing less tolerant species with those that are more adapted to the changing environment (e.g. Mulligan and Gignac, 2002; Rydin, 1993). The model does not consider interspecies competition within a PFT and thus likely overestimates competitive exclusion among PFTs (Gunnarsson et al., 2004; Robroek et al., 2009). For example, species composition had not significantly changed during the study period, whereas the abundance of species has been altered dramatically by long-term atmospheric N deposition in a Czech mountain bog (Hájková et al., 2011). Interspecies competition is also related to environmental factors, such as soil moisture and temperature, that affect the sensitivity of PFTs to N deposition and lead to site-specific responses of vegetation to N deposition (Clark et al., 2007; Limpens et al., 2011; Gunnarsson and Flodin, 2007). For example, *Chamaedaphne calyculata*, which favours dry conditions and is tolerant to a wider range of water table depth than *Rhododendron groenlandicum* (Bubier et al., 2006), showed greater increases in the biomass than the latter with N fertilization (Bubier et al., 2011). Also, the production of *Sphagnum* biomass was more sensitive to N deposition at sites with higher July temperatures and higher annual precipitation (Limpens et al., 2011).

In our model, the changes in the vegetation biomass and composition induced by N deposition were determined by the capability of PFTs to benefit from additionally available

N. This capability included the ability to uptake N, the response of GEP_{max} to N content, and the fate of the assimilated C in maximizing nutrient uptake, light absorption and plant growth. Due to the lack of empirical data that address the above issues, large uncertainties about potential shifts in the vegetation community composition remain. Therefore, in predicting competition among PFTs, it is essential to identify the adaptation and growth strategies of bog species to nutrient poor environments. To do so is a prerequisite for more accurately predicting the path the system will follow in the long-term under conditions of potential competitive exclusion of PFTs. The final plant composition and biomass in the evolving ecosystem are essential for predicting the effect of N deposition on C cycling in the long-term, as suggested by our modelling results.

3 Conclusions

The PEATBOG model, version 1.1, does not consider nutritional limitations other than by N and this way represents a situation as empirically induced by the NPK fertilization scheme. Other evidence has shown that productivity in the Mer Bleue peatland is likely NP co-limited so that the effects of N deposition alone would likely be different from those measured and modelled (Wang et al., 2013; Wang and Moore, 2014; Larmola et al., 2013). The legitimacy of extrapolating our results to atmospheric N deposition is thus limited, and caution should be exercised in generalizing the results.

Acknowledging such reservations, the study demonstrated the ability of the PEATBOG model to correctly reproduce the magnitude of C fluxes under ambient conditions and with increased N deposition levels. The model output deviated from field measurements in its slower decline of moss productivity and biomass and a more rapid increase in GEP with N fertilization. Simulations over 80 years predicted an acceleration of C cycling and greatly enhanced GEP, ER and NEE at higher N deposition levels. The effect of N deposition was closely related to changes in the distribution between the plant functional types and the plant biomass after about 15 years had passed. The response of the C fluxes to elevated N input differed between the plants and the soil. The model results documented an instantaneous increase in the primary production, autotrophic respiration and litter production after N fertilization began. In contrast, a delay of 10 to 15 years occurred with regard to the increase in heterotrophic respiration and CH_4 emissions. Large changes in C fluxes only occurred during the first 20 years of fertilization. Afterwards, C fluxes were predominantly constrained by the vegetation composition and biomass in the new system. From this finding, one may conclude that the short-term experiments that we conducted may not easily be extrapolated to longer time periods.

The original model parameterization resulted in a considerable discrepancy between the short-term simulated and

short-term observed GEP. This discrepancy was diminished by modifying the response of photosynthetic capacity to the N content in vascular plants from linear to unimodal. However, in the model, the unimodal relationship with the photosynthetic capacity of graminoids declines above the leaf N content of 2 g N m^{-2} , equivalent to $0.024 \text{ g N g C}^{-1}$, in the model reduced the inhibition from vascular plants on the growth of mosses and maintained the presence of mosses even at the highest fertilization level. With a linear or unimodal photosynthetic capacity–N content relationship applied to vascular plants, the carbon fluxes deviated along two possible paths that were characterized by dominance of different PFTs, similar to the trajectories that were simulated by analytical models for peatland ecosystem equilibria (Hilbert et al., 2000; Pastor et al., 2002). A graminoid-dominated peatland evolved that was characterized by high GEP, ER and NEE. Alternatively the peatland remained shrub–moss dominated and had smaller GEP, ER and NEE. In the sedge-dominant peatland type, a shift from C gain to C loss was predicted by the model after about 700 years of fertilization and at the highest N fertilization level only. In contrast, in the shrub–moss-dominated peatland type, a net C loss had already occurred within 20 years. The model emphasizes the importance of vegetation dynamics for C fluxes in northern peatlands. This finding is, in our view, the most crucial outcome of the modelling analysis: the vegetation dynamics responds non-linearly to environmental controls and may show different stable states under otherwise similar conditions that will lead to very different outcomes in terms of carbon fluxes and sequestration. More empirical information is thus needed regarding the competition among PFTs and the benefits individual plant functional types may receive from changes in N availability, for example, through increasing photosynthetic capacity.

Appendix A: Equations in PEATBOG 1.1.

1. The original N factor of GEP_{max} (fN_{GEP}) for graminoids and shrubs are linear:

$$fN_{GEP} = \begin{cases} 0 & \text{if } 0 \leq N_{leaf} < N_{min} \\ aN_{leaf} - b & \text{if } N_{min} \leq N_{leaf} < N_{opt}. \\ 1 & \text{if } N_{opt} \leq N_{leaf} \end{cases} \quad (A1)$$

N_{leaf} is the N content in the leaf of each PFT ($g N m^{-2}$).

The parameter a indicates the sensitivity of GEP_{max} to the leaf N content and is assigned to 1.00 for graminoids and 0.65 for shrubs. The parameter b indicates the minimum leaf N content for GEP_{max} and is assigned to -0.60 for graminoids and -0.30 for shrubs. The parameter values are estimated from Fig. 1 in Hikosaka et al. (2004).

2. The modified equations of fN_{GEP} in modifications 1, 2 and 3 for graminoids and shrubs are hyperbolic:

$$fN_{GEP} = \begin{cases} \text{if } 0 \leq N_{foliar} < N_{min} \\ 1 - \tanh(\alpha_1(N_{opt} - N_{foliar})/N_{opt})^{\beta_1} \text{ if } N_{min} \leq N_{foliar} < N_{opt} \\ 1 - \tanh(\alpha_2(N_{foliar} - N_{opt})/N_{opt})^{\beta_2} \text{ if } N_{opt} \leq N_{foliar} < N_{max} \\ 0 \text{ if } N_{max} \leq N_{foliar} \end{cases} \quad (A2)$$

The parameters α and β determine the sensitivity of the photosynthetic capacity (GEP_{max}) to the N content in leaves (N_{foliar}). Large values of α indicate low GEP_{max} and low $N-GEP_{max}$ gradient approaching the minimum and the maximum N content (N_{min} and N_{max}). Large values of β indicate low $N-GEP_{max}$ gradient approaching the optimal N content (N_{opt}). For example, α_2 and β_2 for graminoids in modification 3 are larger than that in modification 2 implying a faster decline of GEP_{max} above the N_{opt} in modification 3 than in modification 2. The N_{min} and N_{opt} for photosynthesis are lower in the shrubs than in the graminoids, considering that shrubs are more limited to N and more conservative in their N cycling. The values of the parameters in Eq. (2) are listed in Appendix 2.

3. Ecosystem respiration (ER):

$$ER = \sum_{j=1}^3 (Rm_{X,j} + Rg_{X,j}) + \sum_{i=1}^{20} Rh_{q,i}. \quad (A3)$$

ER ($g C m^{-2} day^{-1}$) is aggregated from the maintenance respiration (Rm) and growth respiration (Rg) of all C pools in leaf, stem and root of the plants (X) and the heterotrophic respiration (Rh) of the labile and re-

calcitrant C pool (q) in the soil layers (j).

$$Rm_{X,j} = rm_{X,j} C_{struc,X,j} fm_{X,j} fT_{X,j} \quad (A4)$$

$$Rg_{X,j} = rg_{X,j} C_{struc,X,j} fm_{X,j} fT_{X,j} \quad (A5)$$

$$\frac{C_{subs,X,j}}{C_{subs,X,j} + kC_{g,j}} \frac{N_{subs,X,j}}{N_{subs,X,j} + kN_{g,j}} (1 - k_{g,j})/k_{g,j}$$

The respiration rates are calculated from the base respiration rate constants for maintenance ($rm_{X,j}$) and for growth ($rg_{X,j}$), the biomass C ($C_{struc,X,j}$ in $g C$), modifiers of the temperature ($fT_{X,j}$) and moisture ($fm_{X,j}$). The growth respiration is further regulated by the substrate C and N content ($C_{subs,X,j}$, $N_{subs,X,j}$ in $g^{-1} g C^{-1}$) by the PFT-specific $kC_{g,j}$ and $kN_{g,j}$ ($g g C^{-1}$) that represent their growing strategies. The growth efficiency of plants $k_{g,j}$ yields the growth respiration from the biomass C growth.

$$Rh_{q,i} = C_{q,i} kpot_{q,i} fT_{dec,q,i} fm_{dec,q,i} f_{N,i} f_{inhib,i} \left(\frac{1}{CN_{q,i}} - \frac{1}{CN_{crit,q,i}} \right) \quad (A6)$$

$$CN_{crit,q,i} = CN_{mo} \alpha_{q,i} / (\eta q \zeta)$$

The heterotrophic respiration ($Rh_{q,j}$ in $g C m^{-2}$) from labile and recalcitrant C ($C_{q,j}$ in $g C m^{-2}$) is obtained from a potential respiration rate constant ($kpot$ in $g C g C^{-1}$) and modifiers of soil temperature (fT_{dec}), soil moisture (fm_{dec}), end products (f_{inhib}) and nitrogen. The actual CN ratio ($CN_{q,j}$) and the critical CN ratio ($CN_{crit,q,j}$) of the of each soil pool are dynamically obtained. The $CN_{crit,q,j}$ is determined by the CN ratio, the N preferences (α) of the microbe and the efficiency (η) of the microbe for utilizing the labile and recalcitrant soil N. A fraction of decomposition (ζ) is added to the DOC pool which contains all forms of dissolved organic C in this model.

4. The competition for N uptake by PFTs:

$$Nupt_j = \sum_i^{i_{root}} \sum_k^3 Nupt_{i,k}, \quad (A7)$$

$$Nupt_{i,k} = \frac{V_{j,k} N_{conc_{i,j}}}{k_{j,k} + N_{conc_{i,j}}} fCr_{i,j} fTN_{upt_{i,j}} / \left(1 + \frac{kC_{upt_j}}{Cr_{subs_j}} \left(1 + \frac{Nr_{subs_j}}{kN_{upt_j}} \right) \right). \quad (A8)$$

The N uptake rates of graminoids and shrubs are aggregated from the N uptake rates in all the rooting layers (i) of all N species (k): NH_4^+ , NO_3^- and the biologically available DON.

The N uptake rates of each layer of each PFT is obtained using the Michaelis–Menten function with PFT-specific uptake capacity ($V_{j,k}$), half saturation constant

($k_{j,k}$) and the dynamical layer-specific N concentrations ($N_{\text{conc},i,j}$). The uptake rates are modified by the biomass or area of the fine roots ($f_{\text{Crt},i,j}$), a temperature factor ($f_{\text{TNupt},i,j}$), the substrate C and N concentrations in the roots ($\text{C}_{\text{rtsubs},j}$, $\text{N}_{\text{rtsubs},j}$) and the PFT-specific parameters k_{Cuptj} and k_{Nuptj} .

Appendix B

Table B1. Parameter values of GEP_{\max} as hyperbolic functions of foliar N content (N_{foliar}).

Parameter	Description	Graminoids Modification 2	Graminoids Modification 3	Shrubs Modifications 1–3
α_1	Curvature parameter	4	3	2
β_1	Curvature parameter	8	2.5	2
α_2	Curvature parameter	1.5	4	1
β_2	Curvature parameter	1.7	8	2
N_{\min}	Minimum N content in leaves	0.5	0.5	0
N_{\max}	Maximum N content in leaves	–	2.5	–
N_{opt}	Optimal N content in leaves	2.2	2	0.5

The Supplement related to this article is available online at doi:10.5194/bg-12-79-2015-supplement.

Acknowledgements. We greatly acknowledge useful discussions with J. Verhoeven, N. Dise, B. Svensson, B. Robroek, L. Bragazza and P. E. Lindgren that helped clarify concepts in the model development. We further thank P. Lafleur, N. T. Roulet and E. R. Humphreys for facilitating access to data related to the Mer Bleue Peatland, and two referees for their insightful comments. This study is part of the BiodivERsA-PeatBOG project, whose German subproject was funded by the German Ministry of Education and Research (BMBF) grant 01LC0819A to C. Blodau through ERA-net (European Union's 6th Framework). We would like to extend thanks to the Natural Sciences and Engineering Research Council (NSERC) Discovery grant to T. Moore, the Ontario Early Researcher Award to C. Blodau and the National Science Foundation grants DEB-0346625 and DEB-1019523 to J. L. Bubier, S. Juutinen and T. Larmola. Y. Wu was supported by a PhD fellowship of the University of Münster.

Edited by: S. Zaehle

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