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experimental N
deposition

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This discussion paper is/has been under review for the journal Biogeosciences (BG).
Please refer to the corresponding final paper in BG if available.

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

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Received: 16 May 2014 – Accepted: 12 June 2014 – Published: 1 July 2014

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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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 analyze 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 behavior. 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 high tolerance of *Sphagnum* to N deposition in the model. Model performance regarding the 8 year response of GEP and NEE to N was improved by introducing an N content threshold shifting the response of photosynthesis capacity 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 modeling 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 synthesis and fossil-fuel combustion. Despite declining deposition of oxidized N (NO_x), owing to regulations during the last

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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 was predicted to increase two- to three-fold until 2100, especially in regions with intense agricultural land use (Lamarque et al., 2005). 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 0.2 Gt C yr^{-1} of C sequestration, accounting for approximately one fifth of the terrestrial annual net C uptake between 1996 and 2005 (Zaehle et al., 2011). Northern peatlands serve as a major terrestrial C sink and store $547 (473\text{--}621) \text{ Gt C}$ (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 $71 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Yu et al., 2009) with an average of $23 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Loisel et al., 2014). The large storage and small net uptake rate of C may put the C sink function of peatlands under risk when N deposition induces changes in the C cycle.

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). Also the assimilation of C by 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. Meanwhile, the effects of N deposition on ecosystem respiration were found to be mostly insignificant across ecosystems, including wetlands (Liu and Greaver, 2010), in some cases negative (Knorr et al., 2005), yet positive 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

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assumed to be 10% of the C and N in the shrub leaves based on the observed plant cover in the Mer Bleue Bog (Moore et al., 2002). Most of the fundamental algorithms of plant physiology were adopted from the Hurley pasture (HPM) model (Thornley and Verberne, 1989; Thornley et al., 1995; Thornley, 1998). Litter and root exudates are decomposed into dissolved C and N and tracked as DOC, CH₄, CO₂ and DON, NH₄⁺ and NO₃⁻ in the soil. We previously evaluated the model against long-term C and N fluxes at the Mer Bleue Bog, near Ottawa, Ontario (Wu and Blodau, 2013).

Our objective was to examine the capability of the PEATBOG model to simulate the impact of varying N deposition on a C pools and fluxes of a northern bog. We evaluated the simulations against observational data from nitrogen, phosphorus and potassium (NPK) fertilized treatments at the Mer Bleue Bog for a period of 8 years. By investigating and minimizing discrepancies between initial simulations and observations, we identified key parameters, such as the photosynthetic capacities of PFTs that control the response of C cycling to N deposition. In a second step we carried out simulations for a period of 80 years and examined the potential long-term effects of N deposition on the C cycling of an ombrotrophic bog with the original and a modified set of parameters. Based on both types of simulations we analyzed the mechanisms that drive the long-term changes in net C exchange of ombrotrophic bogs, in particular with respect to C sequestration. We also identified empirical knowledge gaps that need to be addressed to predict the future impact of N deposition on the C sequestration of this important type of ecosystem. By looking at the long-term trends, we also evaluated the long-term viability of trends in C fluxes and pools that were observed after 8 years of N fertilization in predicting long-term effects towards the end of 21st century.

2 Material and methods

2.1 Field experiment and empirical data for model evaluation

The NPK fertilization experiment 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 annual mean air temperature is 5.8 °C and the mean precipitation is 910 mm (1961–1990 average; Environmental 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 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., 2005).

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 m × 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.

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 photosynthesis (GEP) was estimated as the sum of NEE

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and ER. 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 bi-weekly 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 dark using an opaque shroud. The measurements were repeated under, 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 in 2005 and 2008. For model evaluation of the CO₂ fluxes, the quadratic relations between the observed GEP and photosynthetic active radiation (PAR) were 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 were averaged over each day to obtain daily observed GEP. The observed and modeled daily GEP, ER and NEE fluxes were averaged for weekly periods and compared.

2.2 Model input, strategy and evaluation

The PEATBOG model, version 1.1, is implemented in stella[®] and calculates daily C and N pools in leaves, stems, fine roots and coarse roots in three PFTs (mosses, graminoids and shrubs), and in labile and recalcitrant soil organic matter pools and in the dissolved phase in soil water (Wu and Blodau, 2013). It consistently emphasizes mass balance principles and the dynamic interplay of production, consumption and translocation of materials throughout the ecosystem. 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 photosynthetically active radiation (PAR), daily snow depth record, annual average and range of air temperature, atmospheric CO₂, CH₄ and O₂ levels, annual N load and biomass distinguished for the different PFTs. The

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daily average precipitation, PAR and snow depth from 1999 to 2009 were derived from continuous (recorded at 30 min interval) 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 modeling strategy encompassed four steps. First we tested the performance of the model that had previously been parameterized, with the exceptions in Table 1, for the *Fluxnet Canada* Mer Bleue site, with 8 years of available data (here called “short-term”) from control plots of the NPK fertilization experiments, as outlined above. The starting point for the vegetation in 1999 was based on the vegetation cover reported for the Mer Bleue Bog (Moore et al., 2002). We used time series and goodness of fit was quantified by the root mean square error (RMSE), linear regression coefficient (r^2), and the degree of agreement (d). Degree of agreement is index range from 0 to 1.0, with an index of 1.0 indicating perfect agreement (Willmott, 1982). The model was then applied to the fertilized treatments. In a second step we identified deviation 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) sources of deviation. 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 LAI of vascular plants. In the third step, we simulated the effect of 80 years (here called “long-term”) of N deposition at the levels investigated and identified fast and slow changes in C pools and fluxes and their causes. In the fourth step the possibility for different long-term stable states of differing C fluxes was explored by running alternative simulations (Modification 1 to 3, Table S1) by changing the responses of photosynthetic capacities of PFTs to tissue nitrogen concentration.

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Model N input was from atmospheric N deposition at $1.5 \text{ g N m}^{-2} \text{ yr}^{-1}$ and N fertilizers. The modeled atmospheric N deposition incorporated wet and dry deposition and was composed of NH_4^+ (30%), NO_3^- (43%) and DON (27%). Fertilization with N in model and field were identical at levels of 1.6, 3.2 and $6.4 \text{ g N m}^{-2} \text{ yr}^{-1}$, equally supplied as NH_4^+ and NO_3^- . Fertilizer was applied within one 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 alone treatments (Larmola et al., 2013; Wang et al., 2013; Wang and Moore, 2014). Therefore, despite the lack of P or K component in the model, the modeling results are hereby referred to as “NPK” to be consistent with the NPK treatment in the field.

For direct comparisons between modeled and measured fluxes we attempted to obtain equivalent fluxes. Simulated ER values were corrected for mid-day air temperature to be compatible to the observed ER rates that had generally been obtained between 9 a.m. and 4 p.m. (Juutinen et al., 2010). The correction was done by calculating the corresponding ER at the maximum daily temperature based on linear relations of air temperature-ER for each year. The simulated daily GEP rates were scaled down by a specific factor for each fertilization simulation to generate the “best fit” to the observations.

We also simulated C and N pools in mosses, leaves, stems, fine roots, coarse roots and the upper 10 cm of peat. The daily values of the pools were averaged from 1 June to 30 October in 2007 to compare with the observations reported in Xing et al. (2010) as an additional evaluation of the model. 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). 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.

3 Results and discussion

3.1 Short-term effect of N deposition on C fluxes

We first compared the weekly averages of the simulated GEP, ER and NEE with the values derived from observation. The simulations captured the seasonal dynamics and 8 year trends of GEP, ER and NEE in control plots and under three N deposition levels. Yet we found a bias towards overestimation of GEP and underestimation of ER (Fig. 1). The simulated weekly average 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 owed to the differing plant coverage and site conditions in the fertilization plots and the nearby *Fluxnet Canada* tower site. The site was located at a distance of approximately 100 m. We used the vegetation cover at the tower site in the model initialization, which encompassed 39 % mosses, 7 % graminoids and 54 % shrubs. The moss and graminoid values were higher and the shrub value was lower than determined on the modeled fertilization plots. The discrepancies between the observed and the simulated initial conditions were thus a result of using another data set for the parameterization and spin-up of the model. Excluding the systematic overestimations in 2001, which may have been caused by initial effects of establishing the experimental plots, the coefficient of determination (r^2) of the simulated and observed GEP ranged from 0.70 to 0.77, and the root mean square errors (RMSE) 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.

A concurrent low degree of agreement (d) and high r^2 and RMSE indicated a systematic bias in the simulations. The correcting factors were determined by establishing the 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 was raised to 0.79 in the control and to approximately 0.9 in the fertilization

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simulations (Fig. 2, Table 2). The model overestimated the LAI of mosses and underestimated the LAI of vascular plants in 10NPK and 20NPK. 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 modeling 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 in the simulated daily averaged ER and NEE, which included respiration during nights and at PPDF below $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$, were not surprising. Thus we corrected the simulated ER for temperature. These factors were obtained as the slopes of the linear relations between the daily average air temperature and ER in each fertilization simulation. The corrected ER and NEE agreed better with the observations. The RMSE, for example, was reduced by $0.69 \mu\text{mol C m}^{-2} \text{s}^{-1}$ and the degree of agreement was raised by 0.2 in the ER model output of the 5NPK simulation (Table 2). The range of the simulated ER was within the large deviation of the observed ER except for in 2008 (Fig. 1). In that year, the observed respiration was larger than in other years also in the control. This finding was likely due to variation of the site-specific conditions, such as the water table depth (WTD) and initial vegetation coverage, which was a result of using another data set for the parameterization and spin-up of the model. The measured summer average WTD from the eddy covariance tower site that was used 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 other factors than WTD might be stronger regulators of ER. Indeed, ER

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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 overestimated the vascular LAI and the *Sphagnum* biomass in 2008 (Table 3). Both deviations likely contributed to the underestimation of ER.

3.2 Short-term effect of N deposition on C pools

Simulated C content in biomass increased in all PTFs with increasing N deposition with exception of the mosses. The latter pool increased only in the 5NPK simulation and declined in 10NPK and 20NPK simulations (Table 3, Fig. 4). 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 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 observations onsite 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 at the end of the 8 year simulation in 2007, i.e. the N effect was larger than in the control (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 over-estimation of production that was observed.

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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. 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 0.024 g cm^{-3} to 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 g cm^{-3} 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 20NPK at 149 g C m^{-2} in the soil organic mass after 8 years of fertilization. In contrast to the underestimated response of moss biomass C to N input, the simulated peat and vascular plants biomass C 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 PK limitation was not considered in the model. The importance of plant coverage for C fluxes was also 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 (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)

and green biomass of the dominant PFTs explained well the site differences in growing season NEE in a site comparison study (Laine et al., 2012). The acceleration of C cycling in the 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).

3.3 Long-term effects of N deposition on C fluxes

After 80 years of simulated N fertilization, the annual average C fluxes among plants, peat and soil water mostly reached new steady states (Figs. 5 and 6). The annual average GEP, ER and NEE were dramatically raised by the addition of N and severe changes occurred only during the first 10 years of fertilization before new balances 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 with higher photosynthetic capacity than mosses and shrubs. The annual ER increased to a lesser extent than GEP, partially as a result of a smaller rise in autotrophic respiration (AR) than GEP at 12, 20 and 21% in 5NPK, 10NPK, and 20NPK, respectively (Fig. 5a). In addition, the effects of N deposition on heterotrophic respiration (HR) showed a significant lag for approximately 10 years in all simulated treatments. Subsequently HR accelerated following the order control < 5NPK < 10NPK < 20NPK, and peaked at 43% above the level of the controls in 20NPK after 80 years (Fig. 6c). The simulated HR in 20N alone had a significant increasing trend beyond the simulation period ($r^2 = 0.3$, $N = 42$, $p < 0.001$) (Fig. S2). Greater increase of GEP in comparison to ER 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 in the 80th simulation year. In the final state, NEE in 10NPK and 20NPK simulations merged and were substantially higher than the NEE in 5NPK simulations (Fig. 5c).

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Promoted by the enhanced GEP, the aboveground litter input increased dramatically from $261 \text{ g C m}^{-2} \text{ yr}^{-1}$ to $555 \text{ g C m}^{-2} \text{ yr}^{-1}$ 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). Regarding belowground heterotrophic processes some other noteworthy effects occurred.

The simulated CH_4 fluxes also increased in all fertilized treatments by a factor of 2–3. This outcome was mostly an effect of the more effective transport of CH_4 by the expanded roots of graminoids (Fig. 7d). The simulated net ecosystem C balance (NECB) that was obtained by subtracting the loss of DOC and CH_4 from NEE, increased greatly from $20 \text{ g C m}^{-2} \text{ yr}^{-1}$ to 87, 150 and $138 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 5, 10 and 20NPK respectively after 80 years of simulation.

Overall, the model predicted the Mer Bleue Bog to become a larger C sink when exposed to long-term N deposition at the high rate of $6.4 \text{ g N m}^{-2} \text{ yr}^{-1}$ (Fig. 7). 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. 7a). 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 the sixth year on in 5NPK (Fig. 7b). 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. 7c and 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% to 90% in 5NPK to 20NPK in roots (Fig. 7e and 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 (Bubier et al., 2011). At the Mer Bleue fertilization exper-

iment, 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. 7g). 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. 7n). The C/N ratio in the upper 40 cm started to decrease after 30 years of fertilization, implying a faster net sequestration of N than C in the peat of the simulated 20NPK treatment (Fig. 7i).

3.4 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 $3.2 \text{ g N m}^{-2} \text{ yr}^{-1}$ N fertilization. The model overestimated GEP in the 10NPK and 20NPK simulations 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 contents in the shoots of plants (2.5 g N m^{-2}) and slopes followed the sequence: shrubs < mosses < graminoids (Fig. 9a). The GEP_{max} of mosses was negatively related to leaf N content and that of graminoids and shrubs were not affected when leaf N exceeded the maximum N content (Fig. 8a). The sequence of slopes and the curvatures of the GEP_{max} -N content relations were 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 at low background N deposition sites (Granath et al., 2009) but to decrease at high background N deposition sites (Van

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Der Heijden et al., 2001). Optimal N content at approximately $0.009 \text{ g N (g dry mass)}^{-1}$ was found in *Sphagnum balticum*, but not in the other two *Sphagnum* species (*S. fallax* and *S. fuscum*) (Granath et al., 2009). 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 relation. In such a relation, 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., 2009).

In contrast, in long-term N fertilization experiments (8–15 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 the adaptation of these long-lived shrubs to a low-N environment hampers their N allocation to photosynthetically active processes when N availability increases. They allocated N to growth, but there were 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 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 relation of shrubs (Fig. 8b, Modification 1) according to the observed lack of relation 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

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in all aspects. Modification 1 resulted in a better fit of the modeled GEP during the first 5 years of fertilization in 20NPK (Fig. 9a). 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 relations of shrubs and graminoids (Modification 2, 3) (Fig. 8c and 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 and 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 photosynthesis 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 our original model formulation was not able to capture this kind of trajectory.

Furthermore, 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 Percy, 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 growth and 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 con-

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tributed 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). Using Modification 3, increases in the growth in graminoid roots and GEP were not sustained due to the limited photosynthesis (Fig. S1b), 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 MB, but it is more abundant on 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 the model. 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.

3.5 The importance of time scale for the effect of N deposition on C fluxes

The simulated annual GEP, ER and NEE showed large variations among the varied GEP_{max} -N relations in the first years and separated into two groups after 20 years of fertilization (Fig. 9d–f). 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 aboveground biomass, and had a signifi-

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cantly higher GEP, ER and NEE than in the shrub-moss dominated type. In the 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. These benefits 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.

Previous work has suggested an occurrence of alternative stable states in peatlands. Using an analytical modeling 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 Hilbert and colleagues' model, which simulated a limited primary production in fens (Hilbert et al., 2000). A dichotomy in vegetation community composition was also predicted by an N-sensitive *Sphagnum*-vascular competition model (Pastor et al., 2001). 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 and 9). However, due to the lack of empirical data regarding the sensitivity of photosynthesis, growth and N uptake to N availability large uncertainties about potential shifts in the vegetation community composition remain.

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 by 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 overestimated 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 favors dry conditions and is tolerant to a wider range of water table depth than *Ledum groenlandicum* (Bubier et al., 2006), showed greater increases in the biomass than the latter with N fertilization (Bubier et al., 2011). The production of *Sphagnum* biomass was more sensitive to N deposition at sites with higher July temperature and higher annual precipitation (Limpens et al., 2011). Therefore it is essential to identify the adaptation and growth strategies of bog species to the nutrient poor environment in predicting the competition among PFTs. 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 modeling results.

3.6 Mechanisms of N deposition impacts on ER

The model simulated a swift response of ER to N deposition via change in autotrophic respiration (AR) and a delayed response of ER via change in heterotrophic respiration (HR). This finding agreed with a time lag that was found in the observations in the responses of ER to N fertilization. A significant increase of ER was observed for the first time at the 20NPK treatment plots after 8 years of fertilization, and was attributed to either an increase in AR from more abundant vascular shoots or an increase in HR stemming from more decomposable fresh litter that was produced by vascular plants

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(Juutinen et al., 2010; Larmola et al., 2013). The model results are thus in line with the short-term and long-term increase of AR and HR, respectively, and explain the mechanism of the observed changes in AR and HR at differing time scales.

The model showed an increase in ER during the first 20 years only. Subsequently two stable states with steady levels of ER existed, regardless of N deposition levels. The shrub-dominated type was characterized by a low ER as a result of a diminished contribution of AR, while in the graminoid-dominated type the opposite occurred (Fig. 9e). Autotrophic respiration was likely limited by the level of plant biomass at the final steady state, which in turn showed little sensitivity to the N deposition levels (Fig. 7a). This interpretation is supported by a strong correlation between plant biomass and AR that was reported from field observation. 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 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). Furthermore, a decrease in the belowground AR was observed in a fertilized boreal spruce forest (Olsson et al., 2005). A large increase in AR is not expected at the Mer Bleue Bog when subjected to increased N deposition in the long-term, taking into account the limit to biomass build-up at the steady state and moderate responses of consumption of photosynthetically assimilated C by AR.

According to the model simulations, the plant-related C fluxes (e.g. AR) changed greatly and immediately after the fertilization during the 10 to 15 years until a new state was attained. In contrast, the soil related C fluxes (e.g. HR) were hardly affected during the first 10 years after which significant changes began to develop (Fig. 6). The delay in the response of HR to N input was associated with the delayed changes of the labile fraction and C/N ratio in the peat (Fig. 7h and i). At N addition levels that are high enough to depress the growth of mosses, potential large increases in HR were, however, suggested by the model.

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The simulated annual HR was averaged for every 11 years, which eliminated the effects of short-term environmental factors. HR was under these conditions highly correlated with the fraction of labile C ($r^2 = 0.97$, $p < 0.001$, $N = 36$) but not with the simulated C/N ratio in the upper 40 cm of peat ($r^2 = 0.07$, $N = 36$) (Fig. S2). The relation between C/N ratio and HR was enhanced but remained insignificant by ignoring the first 33 years ($r^2 = 0.31$, $N = 30$), when the amount of litter input to the soil strongly varied. The relation between HR and C/N ratio of peat was further enhanced and became highly significant when disregarding values from the 5N simulation ($r^2 = 0.90$, $p < 0.001$, $N = 20$) (Fig. S2b). These results reveal that the C/N ratio plays an important role in regulating the HR once the model system is adapted to the N deposition disturbance and organizes itself towards a new steady state. This is especially the case at N inputs above the levels that inhibit the growth of mosses.

Recent reports emphasized the role of intrinsic peat decomposability in regulating HR. In the fertilization plots at the Mer Bleue Bog, higher HR in the long-term was suspected to be related to the raise in decomposability of the fresh litter produced by the vascular plants (Juutinen et al., 2010). In addition, more active root exudation that produces highly biodegradable substrates would contribute to additional microbial respiration in NPK fertilized peat (Larmola et al., 2013). The wetter peat surface observed in the 20NPK plots after a decade of fertilization might also change the peat quality and decomposability (Larmola et al., 2013). Similarly, N fertilization altered the peat quality towards more labile and decomposable and triggered additional HR in a pristine Italian peatland (Bragazza et al., 2012). The increase of the labile peat fraction coincided with decreases of lignin, polyphenol and acid unhydrolyzable residue contents 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, 2009; Bragazza and Freeman, 2007). Our simulations in principle supported this hypothesis but only in the short-term. The enhancement of HR by increase in the labile litter input from the vascular plants ceased after a new state of the system had been established (Fig. 7h). However, with the continuous supply and accu-

mulation of N in peat, the decrease in C/N ratio was prolonged (Fig. 7i). As reduction in C/N ratio of litter has been found to stimulate the decomposition in ombrotrophic bogs (Bragazza et al., 2007; Aerts et al., 2001; Limpens and Berendse, 2003), the continuous decrease in C/N ratio promoted a sustained rise of HR in the long-term under the simulated 20NPK deposition (Fig. 6c).

The outlier in 5N in the linear regression of HR and C/N ratio (Fig. 10b) revealed a N-conserved manner in decomposing *Sphagnum* litter, which leads to more retention of N in the remaining peat, as was suggested by Bragazza et al. (2009). Hence with the change in litter type from *Sphagnum* to vascular, more N may be released from decomposition. The modeling results were in line with this argument, showing abrupt change of the dependence of HR on the soil C/N ratio corresponding to the presence of *Sphagnum*. The simulated average C/N ratio of peat showed an increasing trend in the 5NPK ($r^2 = 0.87$, $N = 12$) and in the 10NPK ($r^2 = 0.90$, $N = 12$) treatments. Raised C/N ratios in these simulations counteracted the stimulation of HR by the raised decomposability of the peat. In contrast, C/N ratio had a trend of declining in the 20NPK simulations ($r^2 = 0.99$, $N = 12$) that reinforced stimulation of HR by litter quality. Consequently, HR showed a continuous increase in the 20N simulation after the first 20 years ($r^2 = 0.89$, $p \ll 0.001$, $N = 10$), but not in the 5NPK and 10NPK simulations where mosses remained present (Fig. 6c).

3.7 Long-term effects of N fertilization on the net ecosystem carbon balance

Large increases in GEP and a relatively small increase in ER resulted in a substantial increase in the net C uptake of the peatland of 78–181 g C m⁻² yr⁻¹ after 80 years of fertilization. The 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). Such high C sequestration rates may not be sustained over even longer periods given the simulated long-term trends in AR and HR. Based on the clearly decreasing trend of C/N ratio after 80 years of fertilization for another 50 years

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($r^2 = 0.95$, $N = 50$) in the 20NPK simulation (Fig. S2a), and the strong correlation between HR and C/N ratio (Fig. 10b), we suspect a continuous increase of HR beyond the simulation period. Considering the coincident stabilization of GEP and AR together with the continuous increase of HR, C loss may occur in the 20NPK simulation at some point beyond the simulation period. With regard to other C losses from the system, CH₄ effluxes increased up to 14 g C m⁻² yr⁻¹ in the graminoid-dominated peatland type in the 20NPK simulation, which was 3.5 times the annual CH₄ emission from the control simulation (ca. 4 g C m⁻² yr⁻¹). The 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). Methane emission was in this case partly limited by the low water table depth in the Mer Bleue Bog. The recently observed raised water table level in the 20NPK treatment plots (Larmola et al., 2013) may facilitate the production of CH₄ and the expansion of graminoids and lead to higher CH₄ efflux from those plots. Carbon loss as dissolved organic and inorganic C changed little by N deposition (not shown). Consequently, the net ecosystem C balance (NECB) in the 20NPK simulation decreased at a rate of 3.2 g C m⁻² yr⁻¹ after the initial increase during the first 10 years (Fig. S2b).

At N deposition rate larger than 3.2 g N m⁻² yr⁻¹, the bog would reach a net C uptake of zero around the year 2700, after more than 700 years of enhanced N availability, at least as predicted by the PEATBOG model. 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 was 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 precipitation. We attribute the slowly falling NECB to the slow decline of the C/N ratio because the fraction of labile peat carbon, that also influences NECB, adjusted more quickly (Fig. 8h). Our results thus imply a continuing positive effect of long-term N deposition on the net C seques-

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tration in the graminoid-dominated scenario before this effect ultimately disappears on the time scale of centuries. However, a rapid release of C from the peatland could occur if it remained shrub-moss dominated when subject to long-term N deposition.

4 Conclusion

5 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 that was modeled. Other evidence has shown that productivity in the Mer Bleue peatland is likely NP co-limited so that effects of N deposition alone would likely be different from those measured and modeled (Wang et al., 2013; Wang and Moore, 10 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. 15 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 CH₄ emission. Large changes in C fluxes only occurred during the first 20 years of fertilization. Afterwards, C fluxes were predominantly constrained by the vegetation 20 composition and biomass in the new system. From this finding one may conclude that 25

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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 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, unimodal relations with photosynthetic capacity of graminoids decline 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 linear or unimodal photosynthetic capacity – N content relation applied on vascular plants, the carbon fluxes deviated along two possible paths that were characterized by dominance of different PFT, similar to the trajectories that were simulated by analytical models on 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 occurred already 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 modeling 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.

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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. 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. Bubier, S. Juutinen and T. Larmola. Y. Wu was supported by a Ph.D. fellowship by the University of Münster.

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Table 1. Updated parameters in PEATBOG 1.1. $M = C, N$; $q =$ 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 .

Name	Description	Value			Unit	Source
		Moss	Gram.	shrub		
Plant						
$Pmax_{20,j}$	Photosynthetic capacity at 20 degrees	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
bPUNE	Intercept of the Photosynthesis rate-leaf N content curve	0	–0.6	–0.3	–	3
$Na_{max,j}$	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_{il_subsN}	Constant of substrate N in litter	0.05			$g N g^{-1}$	8
$rRm_{leaf,j}$	Leaf maintenance respiration rate constant	10	5	5	$g C (kg C)^{-1} day^{-1}$	9
$rRm_{stem,j}$	Stem maintenance respiration rate constant	5	2.5	2.5	$g C (kg C)^{-1} day^{-1}$	9
$rRm_{finert,j}$	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
$r_{exu_{X,j}}$	Exudation rate constant	0.005	0.001	0.001	day^{-1}	Assumed
SOM						
$kCpot_q$	Inherent potential rate constant of decomposition	$kCpot_R = 0.000015$			day^{-1}	Calibrated
k_{fix}	Base N_2 fixation rate	$kCpot_L = 45kCpot_R$			$g N m^{-2} day^{-1}$	12 Calibrated

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.

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Table 2. Regression statistics for the relation between simulated and measured gross ecosystem production (GEP), ecosystem respiration (ER) and net ecosystem exchange (NEE) averaged on a weekly basis in the summer of 2003, 2005 and 2008. GEP was corrected for a LAI related multiplier, ER was corrected for temperature and NEE was obtained from $NEE = GEP + ER$.

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

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Table 3. Simulated and observed soil organic C pool 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*
Modeled								
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 $0.02 \text{ m}^2 \text{ g}^{-1}$.

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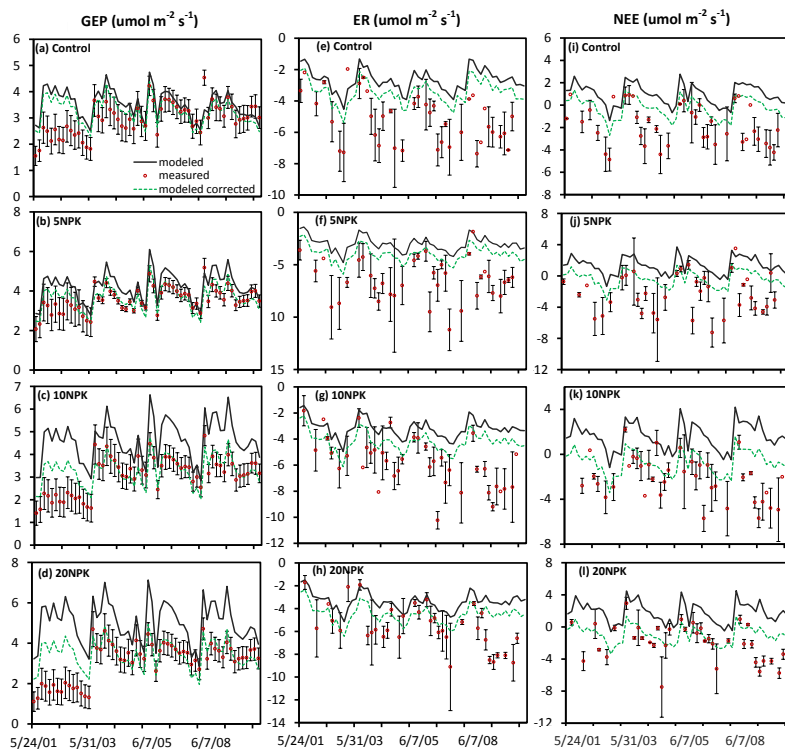


Figure 1. (a–d) Simulated and observed weekly average of gross ecosystem production (GEP), (e–h) ecosystem respiration (ER) and (i–l) net ecosystem exchange (NEE) May to August in 2001, 2003, 2005, 2008. The green dotted lines in represent weekly averaged CO_2 flux corrected for the biomass (a–d), for 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 was K not constrained in the model.

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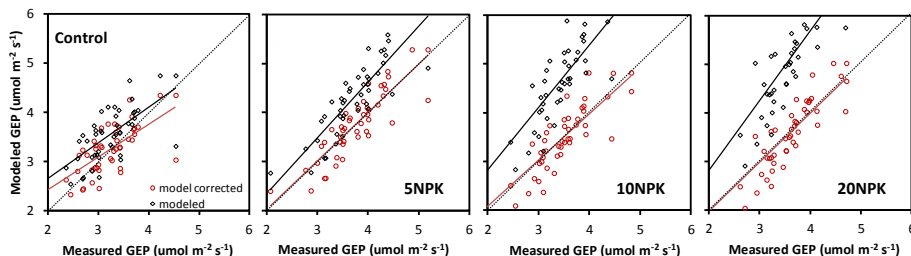


Figure 2. Observed vs. simulated weekly average gross ecosystem production (GEP) in 2003, 2005 and 2008. The black dots and lines represent original simulation and the red dots and lines represent simulation adjusted by a factor producing the “best-fit” (Table 2).

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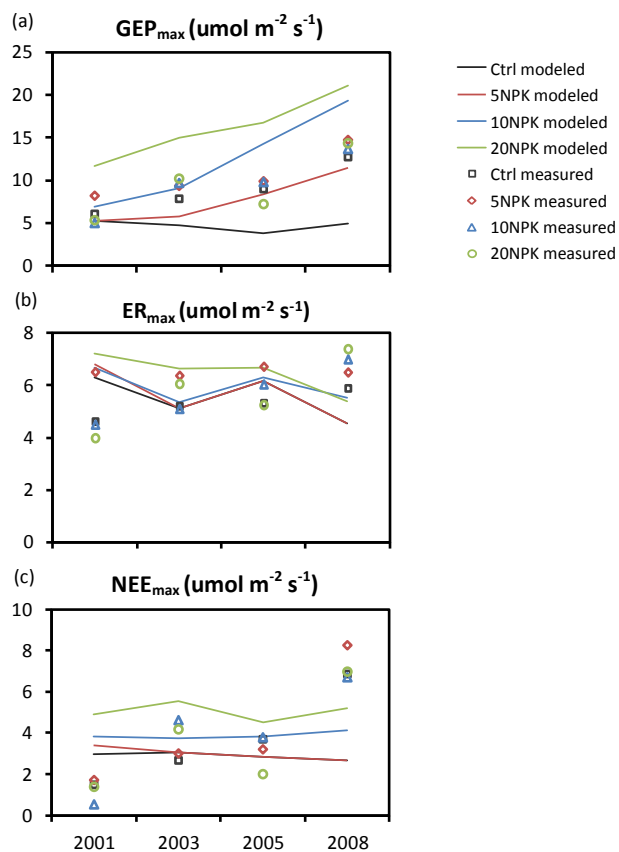


Figure 3. The simulated and measured average (a–c) maximum gross ecosystem photosynthesis (GEP_{max}), ecosystem respiration (ER_{max}) and ecosystem exchange (NEE_{max}) in the fertilized plots at the Mer Bleue Bog in 2001, 2003, 2005 and 2008.

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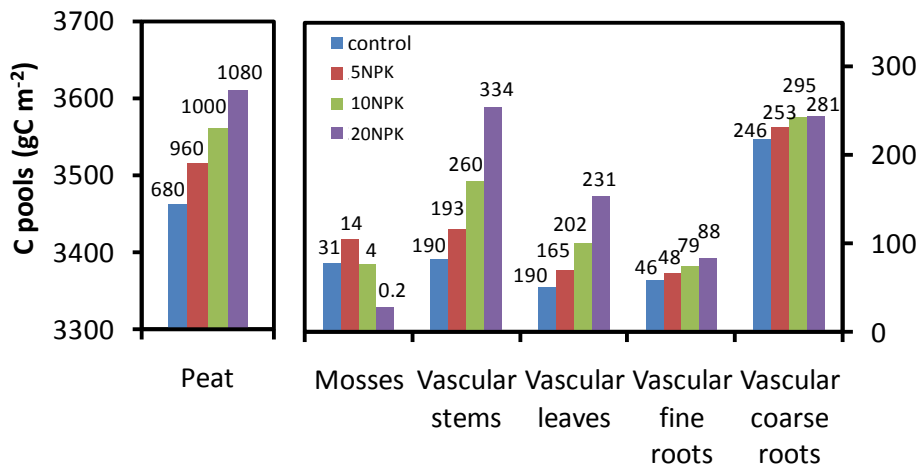


Figure 4. The simulated (bars) and observed (values) summer biomass in plants and peat after 8 years of fertilization. Observed data from Xing et al. (2010) are shown in Table 1.

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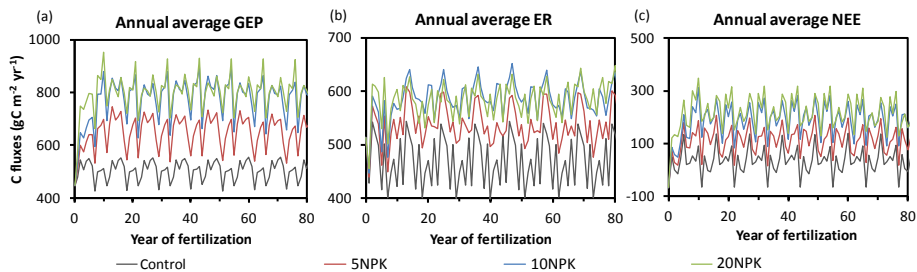


Figure 5. Annual average gross ecosystem production (GEP), ecosystem respiration (ER) and net ecosystem exchange (NEE) over 80 years of fertilization. Positive NEE indicates C gain into the bog.

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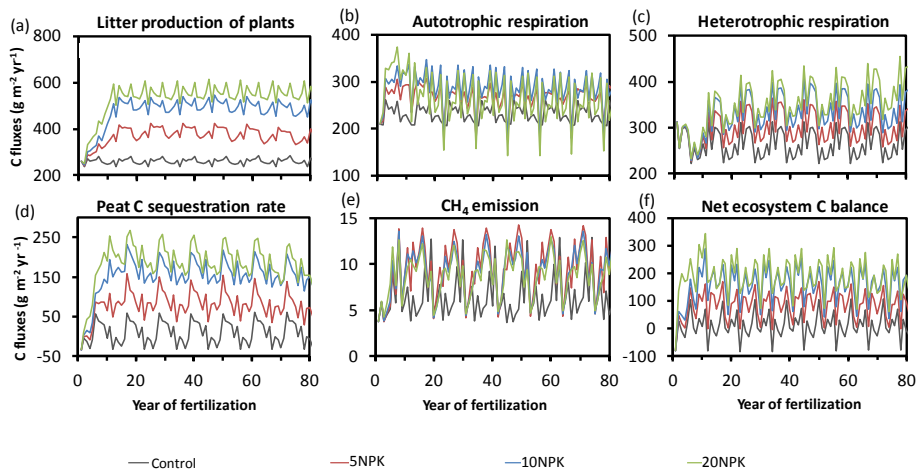


Figure 6. Simulated annual average C cycling rates over 80 years of fertilization.

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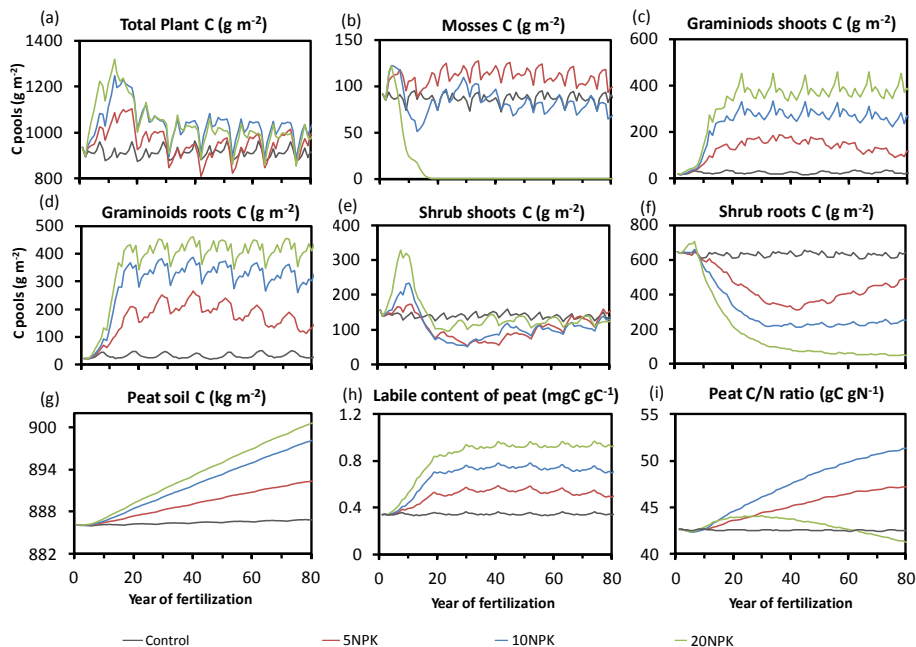


Figure 7. (a–i) Simulated annual average C pools in plants and peat, labile fraction of peat (mg C (g C)^{-1}) and C/N ratio in the upper 40 cm of peat over 80 years of fertilization.

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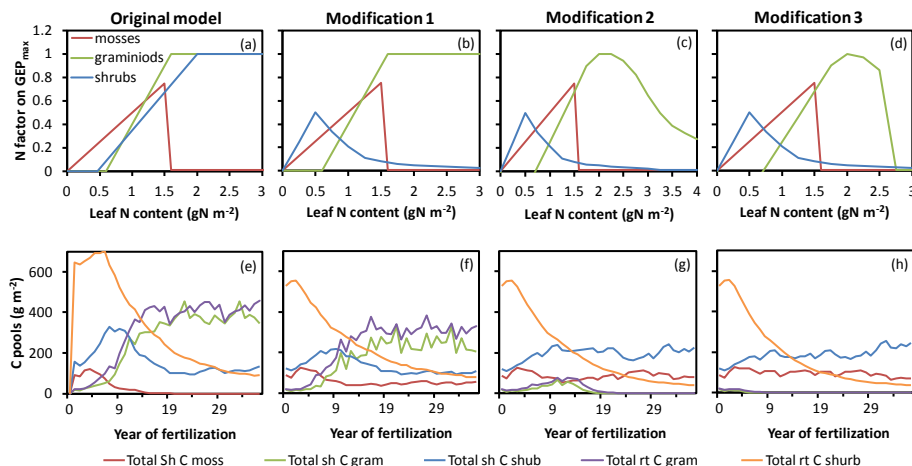


Figure 8. (e–h) Simulated C pools in PFTs during 40 years of fertilization at $6.4 \text{ g N m}^{-2} \text{ yr}^{-1}$ in the simulation with different dependency of photosynthesis on leaf N content (a–d). (a) original model with positive relation between the photosynthetic capacity (GEP_{max}) and N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

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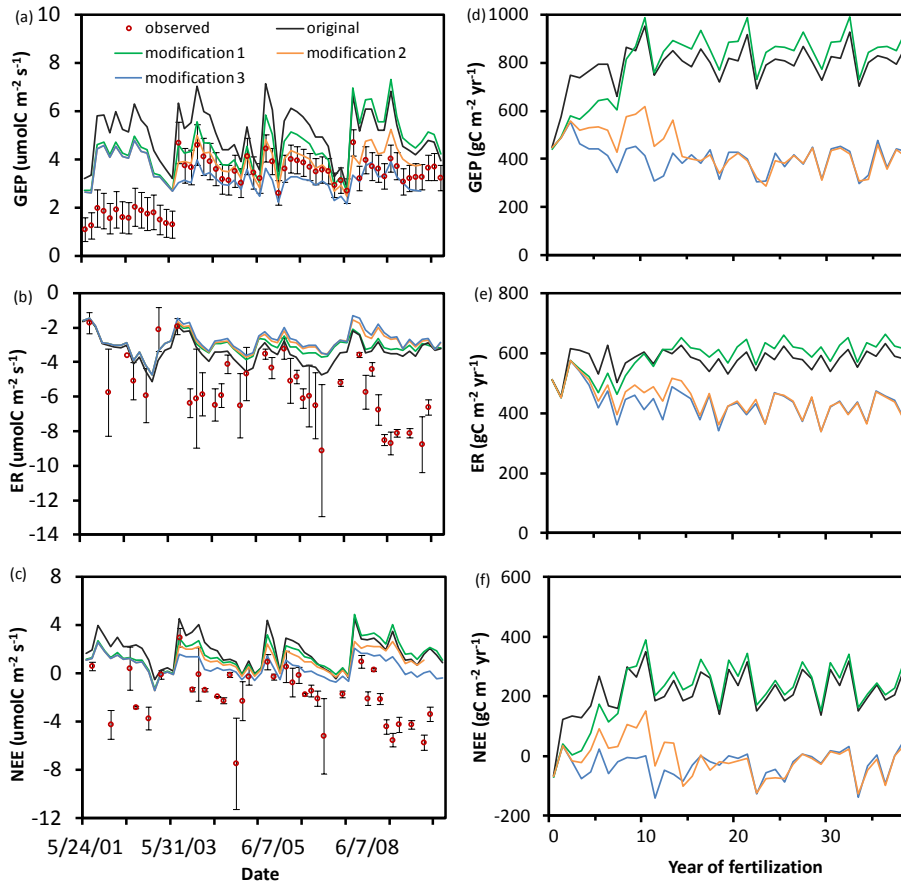


Figure 9. (a–e) simulated and observed gross ecosystem production (GEP), ecosystem respiration (ER) and ecosystem exchange (NEE) from May to August 2001, 2003, 2005, and 2008 fertilized with $6.4 \text{ g N m}^{-2} \text{ yr}^{-1}$. (d–f) simulated annual GEP Modifications (1–3) represent the same modified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

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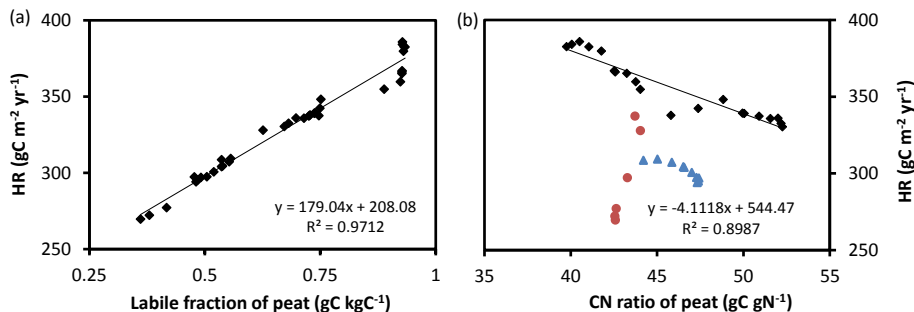


Figure 10. (a) The relationship between modeled annual heterotrophic respiration in the 20NPK treatment (HR) and labile fraction of peat C and (b) between HR and C : N ratio above 40 cm of peat (gC (gN)^{-1}). The values were averaged for each 11 year interval with repeated environmental drivers, black 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.

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