

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

Yuanqiao Wu^{1,5}, Christian Blodau^{1,2*}, Tim R. Moore², Jill Bubier³, Sari Juutinen^{3,4}, Tuula Larmola^{3,4}

¹Hydrology Group, Institute of Landscape Ecology, FB 14 Geosciences, University of Münster, Germany, Robert-Koch-Strasse 26-28, 48149 Münster, Germany.

²Department of Geography, and Global Environmental & Climate Change Centre, McGill University, 805 Sherbrooke St. W, Montreal, Quebec H3A0B9, Canada;

³Department of Environmental Studies, Mount Holyoke College, 50 College Street, South Hadley, Massachusetts 01075, USA;

⁴Current address: Department of Forests Sciences, University of Helsinki, PO BOX 27, FI-00014 Helsinki, Finland;

⁵Current address: Climate Research Division, Environment Canada, 4905 Dufferin Street, Toronto, ON M3H 5T4, Canada.

*Corresponding author, christian.blodau@uni-muenster.de; +1 251-88-30209, Fax: +1 251-83-38338

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 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 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

1 GEP, ER and NEE after 80 years depended on whether a graminoid- or shrub-dominated system evolved. When the
2 peatland remained shrub-*Sphagnum* dominated, it shifted to a C source after only 10 years of fertilization at 6.4g N
3 m⁻² yr⁻¹, whereas this was not the case when it became graminoid-dominated. The modeling results thus highlight the
4 importance of ecosystem adaptation and reaction of plant functional types to N deposition, when predicting the
5 future C balance of N-polluted cool temperate bogs.

6 **1. Introduction**

7
8 Atmospheric nitrogen deposition has been rapidly increasing since the 19th century owing to human activities, such
9 as fertilizer manufacturing and fossil-fuel combustion. Despite declining deposition of oxidized N (NO_x), owing to
10 regulations during the last two decades in Europe and North America, deposition of reduced N (NH_x) that originates
11 from food production remains high (Templer et al., 2012; Rogora et al., 2012; Verstraeten et al., 2012). Globally, N
12 deposition has been projected to increase in many regions until 2100, especially in regions with intense agricultural
13 land use (Lamarque et al., 2011). As a key limiting nutrient for primary production in terrestrial ecosystems
14 (LeBauer and Treseder, 2008), elevated atmospheric N deposition affects the global C cycling and the net
15 sequestration of C (Townsend et al., 1996). Nitrogen deposition was estimated to have caused an increase in global
16 C sequestration of 0.2 Gt C yr⁻¹, accounting for approximately one fifth of the terrestrial annual net C uptake
17 between 1996 and 2005 (Zaehle et al., 2011). Northern peatlands have served as a major terrestrial C sink in the
18 Holocene and currently store 547 (473 - 621) Gt C (Yu et al., 2010), representing about one third of the global C
19 pool. Long-term C accumulation rates of northern peatlands, which are the residue of the fluxes of gross ecosystem
20 production (GEP) and ecosystem respiration (ER), are relatively small and range from 3 to 71 g C m⁻² yr⁻¹ (Yu et al.,
21 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
22 sustained over millennia, may be under risk when N deposition induces changes in the C cycle. For example, a
23 dynamic global vegetation model has simulated a reduction of the maximum annual net primary production in
24 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
25 et al., 2013).

26
27 Current evidence regarding this issue is ambiguous in many aspects. Recent C sequestration rates have been
28 observed to increase in pristine Canadian peatlands undergoing long-term increase of N deposition (Turunen et al.,
29 2004) but to decrease in European bogs (Bragazza et al., 2006) and Alaskan tundra (Mack et al., 2004). Nitrogen is
30 an essential constituent of the carboxylation enzyme (e.g. Rubisco), the light capturing tissues and the plant biomass
31 in general (Evans, 1989, Hikosaka and Terashima, 1995). The maximum leaf photosynthetic rate (GEP_{max}) was
32 found to be strongly and positively related to the leaf N content across C3 plants (Evans et al., 1989). In the
33 extremely nutrient-limited environment, such as peatlands, plants were observed to optimize their growth by
34 increasing the nitrogen-use-efficiencies (Small et al. 1972, Aerts, 1999). As adaptations to the N-poor environment
35 characteristic plant traits emerged, such as slow nitrogen cycling (Urban et al. 1988), small nutrient investment in the
36 photosynthetically active tissue (Wang and Moore, 2014) and large N resorption efficiencies (Wang et al., 2014).
37 The optimization of the growth confounds the effect of N on the photosynthetic capacity and C assimilation of
38 peatland plants. The C assimilation of peatland species was found to be stimulated (Lund et al., 2010), or to remain
39 unaffected (Currey et al., 2011; Gerdol et al., 2008; Bubier et al., 2011) by N enrichment.

40
41 Also the effects of N deposition on ecosystem respiration are uncertain. A meta-analysis suggested a decline of
42 respiration in recalcitrant soil organic matter (Janssen et al., 2010), yet increasing respiration in recently formed litter
43 (Bragazza et al., 2006). The promotion of ecosystem respiration by N deposition was suggested to be potentially
44 substantial due to increased decomposability of peat (Bragazza and Freeman, 2007; Bragazza et al., 2012). Part of
45 such effects would be due to plant community shifts from N-conservative *Sphagnum* species to N-demanding
46 vascular species. Such changes have been observed with long-term atmospheric N deposition (Aaby, 1994;
47 Gunnarsson and Flodin, 2007; Greven, 1992) and experimental N addition (Heijmans et al., 2001; Larmola et al.,
48 2013).

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

7
8 An essential question for clarifying the effects of N deposition on C sequestration in peatlands is whether the
9 changes in GEP and ER will compensate each other. Short-term effects on the scale of years will likely differ from
10 long-term effects on the scale of decades after ecosystem adaptation, for example through shifts in relative
11 abundances of different plant functional types (PFT) and the effects of altered litter quality. Potential long-term
12 decreases in C sequestration of peatlands owing to elevated N deposition from fossil fuel combustion would create
13 an indirect positive feedback to greenhouse gas related climate warming.

14
15 To assess the outlined ecosystem and biogeochemical dynamics we have recently presented the PEATBOG
16 (Pollution, Precipitation and Temperature impacts on peatland Biodiversity and Biogeochemistry) model (Wu and
17 Blodau, 2013), which is further outlined below. In this study, our objective was: (1) to simulate the impact of varying
18 N deposition on a C pools and fluxes of a northern bog; (2) to identify key parameters that determine the effect of N
19 deposition on the C budget of ombrotrophic peatlands; (3) to identify long-term effects of N deposition on the C
20 fluxes of such peatlands and (4) to identify empirical knowledge deficiencies that are important for long-term
21 predictions.

22 23 **2. Material and methods**

24 **2.1 Field experiment and empirical data for model evaluation**

25
26 The environmental setting and model validation were provided by an NPK fertilization experiment that was
27 conducted at the Mer Bleue Bog (45°24'33.9"N latitude, 75°31'7.35"W longitude) located 10 km east of Ottawa,
28 Ontario. The Mer Bleue Bog is a raised acidic ombrotrophic bog of 28 km² with peat depth ranging from 5 to 6 m at
29 the centre to <0.3 m at the margin (Roulet et al., 2007). The vegetation coverage is dominated by mosses (e.g.
30 *Sphagnum capillifolium*, *S. angustifolium*, *S. magellanicum* and *Polytrichum strictum*) and evergreen shrubs (e.g.
31 *Rhododendron groenlandicum*, *Chamaedaphne calyculata*). Some deciduous shrubs (*Vaccinium myrtilloides*),
32 sedges (*Eriophorum vaginatum*), and larch (*Larix laricina*) also appear in some areas (Moore et al., 2002; Bubier et
33 al. 2006). The annual mean air temperature is 5.8 °C and the mean precipitation is 910 mm (1961-1990 average;
34 Environmental Canada). The coldest month is January (-10.8 °C) and the warmest month is July (20.8 °C) (Lafleur et
35 al., 2003). Background N deposition at ca. 1.5 g N m⁻² yr⁻¹ is among the highest in Canada. Wet inorganic N
36 deposition amounted to about 0.8 g m⁻² yr⁻¹ and NO₃⁻ contributed 60 % of this number (Moore et al., 2004).

37
38 The fertilization experiment was established in 2000-2001 (Bubier et al., 2007). Nitrogen was deposited as NH₄NO₃
39 and phosphorus and potassium (P, K) as KH₂PO₄ to triplicate 3 x 3 m plots, every 3 weeks from May to August.
40 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
41 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
42 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
43 times the ambient wet summer N deposition at the Mer Bleue Bog, the field treatments are referred to as 5NPK,
44 10NPK and 20NPK in this study.

45
46 We validated our simulation model against measured data. The net ecosystem exchange of CO₂ (NEE) and
47 ecosystem respiration (ER) were measured during the growing seasons 2001, 2003, 2005, and 2008 using a closed
48 chamber technique. Gross ecosystem production (GEP) was estimated as the sum of NEE and the absolute value of

1 ER (in figures ER shown with negative value). For the results and detailed methods see Bubier et al., (2007) and
2 Juutinen et al. (2010). In short, ecosystem CO₂ exchange was measured weekly or bi-weekly with about 2 – 3
3 minutes closure. The measurements were conducted when the photosynthetic photon flux density (PPFD) exceeded
4 1000 μmol m⁻² s⁻¹, and in the dark using an opaque shroud. The measurements were repeated under full, half, quarter
5 light, and dark conditions from May to August in 2001 and 2003, while CO₂ exchange was measured only under
6 conditions of PPFD > 1000 μmol m⁻² s⁻¹ and dark in 2005 and 2008. In order to produce continuous flux time series
7 for model evaluation of the CO₂ fluxes, the quadratic relations between the observed GEP and photosynthetic active
8 radiation (PAR) were derived for each replicate and each year in 2001 and 2003 and for each replicate of all the
9 measured years in 2005 and 2008, due to the limited number of measurements in 2005 and 2008. The half-hourly
10 PAR levels that were measured at the meteorological station were used to reconstruct half-hourly CO₂ exchange,
11 which then were averaged over each day to obtain daily reconstructed GEP (referred as “observed” in this study).
12 The observed and modeled daily GEP, ER and NEE fluxes were averaged for weekly periods and compared. To
13 estimate C pools of the ecosystem, vegetation samples were collected twice, during the growing seasons of 2000 and
14 2008, and peat cores and soil water were sampled on three occasions from July to October in 2007 (Xing et al.,
15 2010).

16

17 **2.2 The PEATBOG model**

18

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

30

31 Plant physiology is explicitly modeled following the Hurley pasture (HPM) model that contains functionally differed
32 C and N pools in the plants (Thornley and Verberne, 1989; Thornley et al., 1995; Thornley, 1998). Major
33 modifications were made to the HPM model to better represent the strong competition among peatland PFTs for light
34 and nutrients (Appendix A.4). Light competition was modeled using a multiple layer structure of the canopy and
35 assuming an exclusive occupation of PFTs of the canopy layers. Beers Law was applied to determine the descending
36 light level from the high to low canopy following the sequence: graminoids > shrubs > mosses. The N uptake of
37 PFTs was modeled by considering the interception of deposited N by mosses and the uptake of N by vascular roots.
38 Mosses were assumed to take up 95% of the deposited N unless P limitation occurs in mosses. When mosses are
39 saturated with N at 20 mg N g⁻¹ biomass, larger quantities of N enter the soil water and become available to vascular
40 plants. The competition of the dissolved N among the vascular PFTs is conceptualized through the architecture of the
41 roots and the uptake capacity of the three N sources (NH₄⁺, NO₃⁻ and DON) that are modeled in each soil layer.
42 Michaelis-Menten equations were used to quantify the N uptake from each soil layer and PFT. In the current version
43 the maximum uptake rate (V_{max}) is larger and the half saturation constant (K_m) lower for NO₃⁻ than for NH₄⁺, owing
44 to the different uptake mechanisms (Kirk and Kronzucker, 2005). Shrubs and graminoids were not distinguished for
45 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
46 PFT, which in turn is determined by the N use-efficiency and turnover of N pools in the PFT. The model is thus able
47 to model the N uptake dynamically and avoids hard-coded differences between PFTs in terms of N dynamics. Light
48 competition also interacts with the N competition through biomass growth and plant N content.

49

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

13 **2.3 Model input, strategy and evaluation**

14
15 Model N input was from atmospheric N deposition at 1.5 g N m⁻² yr⁻¹ and N fertilizers. The modeled atmospheric N
16 deposition incorporated wet and dry deposition and was composed of NH₄⁺ (30 %), NO₃⁻ (43 %) and DON (27 %).
17 Fertilization with N in model and field were identical at levels of 1.6, 3.2 and 6.4 g N m⁻² yr⁻¹, equally supplied as
18 NH₄⁺ and NO₃⁻. Fertilizer was applied within one day in intervals of 21 days from May 1st to August 31st.
19 Simulations were conducted with C:N interactions and without constraints posed by P or K availability in order to
20 make the model output comparable with the NPK treatments in the field experiment. The P and K limitation on
21 plants at the Mer Bleue Bog was alleviated in the experimental NPK fertilizer treatments, compared to the concurrent
22 N alone treatments (Larmola et al., 2013; Wang et al., 2013; Wang and Moore, 2014). Therefore, despite the lack of
23 P or K component in the model, the modeling results are hereby referred to as “NPK” to be consistent with the NPK
24 treatment in the field. The annual C and N fluxes between plant, soil and water were summed from the daily
25 simulations to examine the trends of C and N cycling in the long-term.

26
27 The modeling strategy encompassed four steps. The first two steps simulated an 8-year period (here referred to as
28 “short-term”) and steps three and four simulated an 80-year period (here referred to as “long-term”). First we tested
29 the performance of the PEATBOG 1.1 version at the *Fluxnet Canada* Mer Bleue site. To this end “short-term” data
30 from control plots of the NPK fertilization experiments were employed. The initial state of the vegetation in 1999
31 was based on a vegetation cover as reported for the Mer Bleue Bog earlier (Moore et al., 2002). We used time series
32 and goodness of fit that was quantified by the root mean square error (RMSE), linear regression coefficient (r^2), and
33 the degree of agreement (d). Degree of agreement is index range from 0 to 1.0, with an index of 1.0 indicating
34 perfect agreement (Willmott, 1982).

35
36 In the second step, the model was applied to the NPK fertilized treatments. We examined the deviations of C fluxes
37 in model and empirical results and identified the external (e.g. difference in temperature inputs; differences between
38 daily average values in model and empirical measurements under selected PPFD conditions) and internal (e.g.
39 underestimation of biomass and leaf area index (LAI) of shrubs in the model) drivers of the deviations. As part of
40 this procedure it was tested whether these deviations could simultaneously be mitigated in all treatments by
41 implementing correction factors relating to temperature and coverage of *Sphagnum* and LAI of vascular plants. The
42 simulated ER was scaled up for mid-day air temperature to be compatible to the observed ER that was generally been
43 obtained between 9 am and 4 pm (Juutinen et al., 2010). The correction factor was obtained by calculating the
44 corresponding ER at the maximum daily temperature based on linear relations of air temperature-ER for each
45 treatment. The correcting multipliers of ER were distinguished for each treatment to eliminate the effect of other
46 factors, such as leaf area indexes and biomass, on the relation between ER and T. The simulated daily GEP was
47 scaled down by a specific factor for each fertilization simulation to generate the “best fit” to the observations. By
48 investigating and minimizing discrepancies between initial simulations and observations, we identified the key
49 parameters to be the relation between photosynthetic capacities and N content (GEP_{max-N}) in PFTs that control the

1 response of C cycling to N deposition. In the model, the total peat C pool was assumed to be constant in the upper 19
2 layers but variable in the 20th layer from 95 cm peat depth to the bottom of the peat column. This structure was meant
3 to simplify the calculation of peat C sequestration in the bottom layer. In order to calculate the C stored in the upper
4 10 cm of the peat during the summer of 2007, we added the accumulated C inflow from plant litter to the C stored in
5 peat on June 1st and then subtracted the C outflow for peat decomposition during the period from June 1st to October
6 30th.

7
8 In the next two steps, we explored how the “long-term” C fluxes were affected by N deposition. Furthermore the
9 importance of the controls on the response of C cycling to N deposition that had been identified in the “short-term”
10 simulations was investigated as well. In the third step, we simulated the effect of 80 years of N deposition at the
11 fertilization levels of the field site and focused on the time scale of change in C pools and fluxes and its causes. In
12 the fourth step, multiple “long-term” simulations were carried out by varying photosynthetic response to nitrogen
13 content in foliar tissue of the PFTs, as given by the key parameter GEP_{max-N} (Modification 1 to 3, Table S1). By
14 examining the trajectories of variables of interest in the long-term simulations, we evaluated the possible trends in C
15 fluxes and pools towards the end of 21st century.
16

17 3. Results and Discussion

18 3.1 Short-term effect of N deposition on C fluxes

19
20 We first compared the weekly averages of the simulated GEP, ER and NEE with the reconstructed values derived
21 from observation during the summer in 2001, 2003, 2005 and 2008 (Fig. 1). The simulations captured the seasonal
22 dynamics and 8-year trends of GEP, ER and NEE in control plots and under three N deposition levels. Yet we found
23 a bias towards overestimation of GEP and underestimation of ER and NEE (Fig. 1). The simulated GEP increased
24 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
25 best predicted the effects of smaller N addition as Willmott’s agreement (d) was highest in 5NPK and lowest in
26 20NPK (Table 2). The simulated GEP in 2001 was overestimated also in the control, which is likely a result of
27 spinning up the model with the data set from the Fluxnet Canada tower site other than the fertilization plots. The
28 plots were located at a distance of approximately 100 meters from the tower site, with which the model has been
29 initialized for 39% mosses, 7% graminoids and 54% shrubs. The initial biomass and coverage of moss and
30 graminoids on the fertilization plots were higher and of shrubs lower than at the tower site and in the model.
31 Excluding the systematic overestimations in 2001, the coefficient of determination (r^2) of the simulated and observed
32 GEP ranged from 0.70 to 0.77, and the root mean square errors (RMSE) were between 0.69 and 1.59 $\mu\text{mol C m}^{-2} \text{ s}^{-1}$
33 ($N = 43$). Larger discrepancies occurred at higher N levels.
34

35 Overall, the concurrent low degree of agreement (d) and high r^2 and RMSE between the simulated and observed GEP
36 indicated a systematic bias in the simulations. The correcting factors were determined by establishing a linear slope
37 between simulation output and the observations (Table 2). After applying the factors, the RMSE decreased to 0.34 –
38 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
39 simulations (Fig. 2, Table 2). The model overestimated the LAI of mosses and underestimated the LAI of vascular
40 plants in 10NPK and 20NPK (Table 3). The discrepancies in the simulated and observed moss cover and the vascular
41 LAI together explained 86 % of the correcting factors. This outcome indicated a high importance of accuracy of
42 plant composition and biomass when modeling C fluxes.
43

44 Simulated weekly average ER and NEE agreed more with the observations at the beginning of the fertilization and
45 less so in 2008 (Fig. 1e-1h). The RMSE of the simulated ER ranged from 2.26 $\mu\text{mol C m}^{-2} \text{ s}^{-1}$ in 20NPK to 3.07
46 $\mu\text{mol C m}^{-2} \text{ s}^{-1}$ in 5NPK, which was small compared to the standard deviation of the observation ranging from 2.5 to
47 5.4 $\mu\text{mol C m}^{-2} \text{ s}^{-1}$. The overestimation of ER that included respiration during night time was not surprising. Thus we

1 corrected the simulated ER for temperature by the slopes of the linear relations between the daily average air
2 temperature and ER in each simulation. The corrected ER and NEE agreed better with the observations. For the ER
3 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
4 (Table 2). The range of the corrected simulated ER was within the large deviation of the observed ER except for in
5 2008, when the observed respiration was larger than in other years also in the control (Fig. 1). This was likely due to
6 variation of the site-specific conditions, such as the water table depth (WTD) and the vegetation cover. The measured
7 summer average WTD from the eddy covariance tower site for model initialization was closer to the peat surface (-
8 35 cm) in 2008 than in the other years. In contrast to the observations from the fertilization plots, ER was therefore
9 expected to be lower in 2008 than in the other years. This was even the case for the 20NPK plots, where a significant
10 rise in WTD (-19 cm) was observed in the summer of 2008 (Juutinen et al., 2010). On the other hand, the simulated
11 ER at mean WTD (-35 cm) was lower than the observed ER at mean WTD (-19 cm), suggesting other factors than
12 WTD might be stronger regulators of ER. Indeed, ER was found to be the most related to factors indicating more
13 vascular biomass and less *Sphagnum* biomass, whereas the correlation between ER and WTD was only 0.28
14 (Juutinen et al., 2010). The model underestimated the vascular and overestimated the *Sphagnum* biomass in 2008
15 (Table 3). Both deviations likely contributed to the underestimation of ER.

16 3.2 Short-term effect of N deposition on C pools

17 Simulated C content in biomass generally increased in shrubs and grasses with increasing N input but not in mosses.
18 Carbon in moss biomass increased only in the 5NPK simulation and declined in the 10NPK and 20NPK simulations
19 (Table 3, Fig. 3). The simulated moss coverage declined more slowly than in the observations (NPK treatments) and
20 was only impaired from 2005 on, when it had nearly disappeared in the 20NPK treatment in the experiment (Juutinen
21 et al., 2010). This may be caused by the fact that we simulated impacts of N, while the experiments have shown that
22 the impact of the NPK treatment is stronger, i.e., shrub growth is enhanced more strongly, than that of the N-only
23 treatment (Larmola et al. 2013). The initial overestimate of moss biomass and surface cover and underestimate of
24 shrub biomass compared to observations onsite likely contributed to the delay in moss disappearance (Table 3). The
25 simulated aboveground biomass C of vascular plants increased with N load, following the sequence of control <
26 5NPK < 10NPK < 20NPK. In stems and leaves biomass C increased from 83 and 50 g C m^{-2} in the control to 254 g
27 C m^{-2} and 153 g C m^{-2} in 20NPK. In comparison, the belowground biomass was less affected by N deposition,
28 especially with respect to coarse roots that increased the most in the 20NPK simulation at 12 % (Table 3). Both the
29 simulated leaves and stems of vascular plants tripled in the 20NPK simulations compared to control simulation at the
30 end of the 8-year simulation in 2007 (Table 3). The model uses fixed leaf/stem ratios of vascular plants and does not
31 take into account the observed larger biomass increases in stems than in leaves (Juutinen et al., 2010). This likely
32 added to the overestimation of production of mosses and underestimation of negative effects of vascular plants on
33 *Sphagnum* mosses (see also Chong et al. 2012).

34 The simulated peat C pool was larger than the observation mainly due to a higher bulk density in the model than
35 observed in the control and treatment plots, where the average bulk density of the upper 10 cm peat was 0.017 g cm^{-3}
36 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
37 comparison, the bulk density in the model was stable for each peat layer and was averaged from an earlier
38 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,
39 2002). The simulated peat C pool did not show the abrupt temporal changes that characterized the plant C pool, but a
40 steady trend of increases with raised N input. The greatest increase occurred in 20NPK at 149 g C m^{-2} in the soil
41 organic mass after 8 years of fertilization. As the model considers litter as peat, the simulated increase in the C pool
42 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
43 plots compared to 49 g C m^{-2} in the control plot (Bubier et al., 2007). Even though our model underestimated C in
44 moss biomass C in response to N input, the simulated relative change in carbon content in the peat and vascular plant
45 biomass highly agreed with the observations, with coefficients of determination (r^2) ranging from 0.70 to 0.97 ($N =$
46 4) (Table 3).

47

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

15 **3.3 Long-term effects of N deposition on C pools**

16
17 Overall, the model predicted the Mer Bleue Bog to become a larger C sink when exposed to long-term N deposition
18 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
19 of 911 to 1045 g C m^{-2} in 2080, regardless of simulated N treatment, after steady state was attained (Fig. 4a). The
20 allocation of C among PFTs and their parts was substantially altered, though. After an initial surge the C pool in
21 mosses declined from the fourth year on in 20NPK and the sixth year on in 5NPK (Fig. 4b). It re-stabilized in 5NPK
22 and 10NPK at equally higher levels than in the control after 20 years of fertilization. In the simulated 20NPK
23 treatment moss continuously declined to extinction after 15 years of fertilization (C pool in mosses $< 1 \text{ g m}^{-2}$). Carbon
24 in both the shoots and roots of graminoids expanded concurrently to the decline of C in mosses, following the
25 sequence of control $< 5\text{NPK} < 10\text{NPK} < 20\text{NPK}$ (Fig. 4c, 4d). From a small contribution of 7 % (shoots) and 4 %
26 (roots) of C in the plants, graminoids became the dominant PFT and ultimately stored most C in the simulated
27 10NPK and 20NPK treatments. However, the increase of C in the shrub shoots and roots was sustained only during
28 the first 5 years and decreased by approximately 25 % to 90 % in 5NPK to 20NPK in roots (Fig. 4e, 4f) after 80
29 years of fertilization. This finding does not consider larger growth increases in deciduous shrubs compared to
30 evergreen shrubs that were reported in field investigations (Larmola et al., 2013). At the Mer Bleue fertilization
31 experiment, graminoids are scarce and only some scattered *E. vaginatum* occur. However, the ferns *Dryopteris*,
32 *Cystopteris* and *Thelypteris* were established and contributed up to 24% to the abundance of vascular plant leaves in
33 the 20NPK plots after 11 years of fertilization (Larmola et al., 2013).

34
35 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
36 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
37 additional vertical peat growth (Fig. 4g). Along with an increase in C sequestration, the labile C content of peat
38 increased substantially once graminoids dominated the litter source. In addition, the C/N ratio of peat in the upper 40
39 cm widened in the 5NPK and 10NPK simulations and at the beginning in the 20NPK simulation as well (Fig. 4n).
40 The increasing C/N ratio in the 5NPK, 10NPK and at the beginning of the 20NPK was a result of a faster net
41 sequestration of C than N in the peat. The limited N sequestration in the peat subject to low N inputs was attributed
42 to the living moss layer that effectively retained most of the N at the ground surface (Fig. 4b). When mosses were
43 saturated and eliminated from the vegetation community, N filtration failed and the N that had previously been
44 retained by the mosses was transferred into the peat N pool. Ratios of C/N ratio in the peat thus began to decrease
45 after 30 years in the 20NPK treatment (Fig. 4i).

46 **3.4 Long-term effects of N deposition on C fluxes**

47
48 Annual average GEP, ER and NEE were raised by the addition of N and severe changes occurred only during the

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

6
7 Ecosystem respiration consists of two decoupled C fluxes, autotrophic respiration (AR) and heterotrophic respiration
8 (HR). In our model, autotrophic respiration was limited by the level of plant biomass, which showed little sensitivity
9 to the N deposition levels at the final states (Fig. 4a). This interpretation is supported by a strong correlation between
10 plant biomass and AR. For example, lower ER was found in the 20NPK fertilization plots than in others in 2005,
11 when the increase in the biomass of vascular plants had not yet compensated the loss of *Sphagnum* biomass (Juutinen
12 et al., 2010). Evidence of a moderate AR response to N was found in *Eriophorum vaginatum* after 5 years of N
13 fertilization at 5.6 g N m⁻² yr⁻¹ in a Scottish ombrotrophic bog (Currey et al., 2011). In the long-term, subtle changes
14 in AR is expected at the fertilization plots in the Mer Bleue Bog, taking into account the limit to biomass build-up at
15 the steady state and moderate responses of consumption of photosynthetically assimilated C by AR.

16
17 In contrast, the effects of N deposition on HR showed a significant delay for approximately 10 years in all simulated
18 treatments. The simulated delay was in line with the 9-year period before the initial significant increase of ER was
19 observed in the 20NPK treatment plots (Larmola et al. 2013). The lagged responses of HR to N deposition
20 corresponded to the expansion of vascular plants and increased litter production (Juutinen et al., 2010, Fig. 4). After
21 the first 10 years, HR accelerated in the order control < 5NPK < 10NPK < 20NPK, and peaked at 43 % above the
22 level of the controls in 20NPK after 80 years (Fig. 6c). The simulated increase in HR in 20NPK was significant
23 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
24 the decomposability of the fresh litter from the vascular plants had increased in the experiments (Juutinen et al.,
25 2010).

26
27 The simulated annual HR was averaged for every 11 years, which was the length of the repeated climatic input, to
28 eliminate the effects of short-term environmental factors. HR was, under these conditions, highly correlated with the
29 fraction of labile C ($r^2 = 0.97$, $p < 0.001$, $N = 36$) (Fig. 7a). Recent reports have emphasized the role of intrinsic peat
30 decomposability in regulating HR. The increase of the HR coincided with declining lignin, polyphenol and acid
31 unhydrolyzable residue content in peat, as has been found both in N fertilization experiments (Aerts et al., 2006;
32 Limpens and Berendse, 2003; Breeuwer et al., 2008) and along gradients of chronic N deposition (Bragazza et al.,
33 2006; Bragazza and Freeman, 2007; Bragazza et al., 2009). In addition to the fresh litter, more active root exudation
34 can also produce highly biodegradable substrates to trigger additional microbial respiration in NPK fertilized peat
35 (Larmola et al., 2013). Changes in the peat hydraulic conditions may also change the peat quality and
36 decomposability and have been observed on the 20NPK plots after a decade of fertilization (Larmola et al., 2013).
37 Evidence of increases in HR following an increase in peat decomposability has been found also in pristine peatlands,
38 where N fertilization altered the peat quality towards more labile and enhanced HR (Bragazza et al., 2012).
39 Moreover, stimulation of peat decomposability due to N fertilization has been suggested also in Arctic tundra (Mack
40 et al, 2004). On the other hand, the modeling results here also suggest a maximum level of HR that would be
41 approached when the system has established a new stable state with little change in either litter production or
42 vegetation composition (Fig. 4a- 4f, Fig. 6a).

43
44 The correlation between simulated HR and the C/N ratio of peat was poor when all data were included ($r^2 = 0.07$, $N =$
45 36) (Fig. 7b) and only somewhat improved when excluding the first 33 years with strongly varying litter input to the
46 soil ($r^2 = 0.31$, $N = 30$). The relation was on the other hand much stronger and highly significant when disregarding
47 values from the 5NPK simulation ($r^2 = 0.90$, $p < 0.001$, $N = 20$) (Fig. 7b). The outlier of 5NPK in the regression of
48 HR and C/N ratio revealed a non-linear change in the N retention of the peat corresponding to the vegetation shift
49 from *Sphagnum*-shrub dominated to graminoid dominated. The conservative decomposition of *Sphagnum* litter led to

1 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
2 suggested by Bragazza et al. (2009). Following the change in litter type from *Sphagnum* to vascular in 10NPK ($r^2 =$
3 0.90 , $N = 12$), more N per C was released from decomposition and the C/N ratio of peat increased (Fig. 4i). In the
4 only simulation where mosses were diminished in the system, 20NPK, the increase of C/N ratio in peat ceased and
5 even reversed following the establishment of grasses as predominant PFT ($r^2 = 0.89$, $p \ll 0.001$, $N = 10$) (Fig. 4i).
6 This reversal reflects the direct N input from deposition without the “moss filter” (Fig. 4b). Meanwhile, the strong
7 inverse correlation between HR and C/N ratio holds true in the vascular dominated systems (10NPK and 20NPK) (r^2
8 $= 0.99$, $N = 12$), suggesting a potential increase of HR with the diminishing C/N ratio if the high N deposition
9 sustained beyond the simulation period (Fig. 4i).

10
11 In the simulations GEP increased more strongly than ER, which resulted in a large increase of NEE from 45 g C m^{-2}
12 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.
13 Towards the end of this period, NEE in 10NPK and 20NPK simulations converged and were substantially higher
14 than the NEE in 5NPK simulations (Fig. 5c). Promoted by the enhanced GEP, the aboveground litter input increased
15 substantially 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
16 in ER, annual C sequestration was raised by a factor of 2 – 4 (Fig. 6d). A large increase of C sequestration has not
17 been observed in the fertilization experiment that has to date sustained a vegetation community dominated by shrubs
18 (see Juutinen et al. 2010, Larmola et al. 2013). Accordingly, modified simulations with predominance of shrubs and
19 mosses led to much smaller C sequestration rates (see section 3.6). The deviation between modeled and observed C
20 sequestration rates in the first decade of the experiment thus hinges on the difference in the predominant PFT
21 between model and reality. Regarding belowground heterotrophic processes, some other noteworthy effects
22 occurred. The simulated CH_4 fluxes also increased in all fertilized treatments by a factor of 2 – 3 up to $14 \text{ g C m}^{-2} \text{ yr}^{-1}$
23 1 . This outcome was mostly an effect of the more effective transport of CH_4 by the expanded roots of graminoids
24 (Fig. 6e). The increased ratio was analogous to the observed 2 to 4 fold difference between the growing season daily
25 CH_4 emission rates in the graminoid-dominated collars and the shrub-dominated collars during 2004 to 2008 in the
26 Mer Bleue Bog (Moore et al., 2011). Carbon loss as dissolved organic and inorganic C changed little by N deposition
27 (not shown).

28
29 The simulated net ecosystem C balance (NECB) that was obtained by subtracting the loss of DOC and CH_4 from
30 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
31 80 years of simulation. The simulated C sequestration was above the reported long-term range in boreal peatlands of
32 16 to $23 \text{ g C m}^{-2} \text{ yr}^{-1}$ (e.g. Turunen et al., 2004), and similar to the reported values for short-grass steppe and wet
33 tundra of 117 and $141 \text{ g m}^{-2} \text{ yr}^{-1}$ (Knapp and Smith, 2001). It is noteworthy that the N deposition level used in this
34 study was much higher than under natural conditions and predicted future N deposition levels up to $2 \text{ gN m}^{-2} \text{ yr}^{-1}$.
35 Such high C sequestration rates, however, may not be sustained over even longer periods given the potential increase
36 of HR in our simulation. Corresponding to the decrease C/N ratio as discussed above, a linear decreasing of NECB
37 was clear and C loss was predicted for 20NPK simulation: The slope of $0.28 \text{ g C m}^{-2} \text{ yr}^{-1}$ of the NECB simulation
38 resulted in a net C uptake of zero after about 700 years of N fertilization (Fig. S2). The slow response in the C
39 sequestration of the peatland to N deposition was similar to the slow response of peatlands to climatic disturbances
40 predicted by the HPM model, in which 500-600 years was needed for the peatland to cease C sequestration (Turetsky
41 et al., 2012). The results from the HPM model suggested the importance of mosses for maintaining the cool
42 environment and for buffering water table variations upon changes in precipitation. In this study, mosses were also
43 essential for peat to sustain a high C/N and subsequently.

44 **3.5 Mechanisms underlying simulated effects of N deposition on GEP and NEE**

45
46 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
47 fertilization. The model overestimated GEP in the 10NPK and 20NPK simulations compared to observations during
48 the first 8 years, owing to a greater increase in the graminoid biomass and the higher photosynthetic capacity
49 (GEP_{max}) of graminoids and shrubs than of mosses. In the current model version, GEP_{max} was positively and linearly

1 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
2 sequence: shrubs < mosses < graminoids (Fig. 8a, Appendix A). The GEP_{max} of mosses was negatively related to leaf
3 N content and that of graminoids and shrubs were not affected when leaf N exceeded the maximum N content (Fig.
4 8a). The sequence of slopes and the shape of the GEP_{max} -N content relations were based on observations across
5 growth forms and N gradients.

6
7 Specifically, the photosynthetic capacity in *Sphagnum* mosses was found to increase with N content in tissue with
8 species-specific yields and without increases in production (Granath et al., 2009a, 2009b, Granath et al., 2012). The
9 optimal N content for GEP_{max} was suggested to occur at approximately 12.9 mgN g^{-2} and for photosynthetic N-use-
10 efficiency at 9.1 mgN g^{-2} in *Sphagnum balticum*, but not in the other two *Sphagnum* species (*S. fallax* and *S. fuscum*)
11 (Granath et al., 2009b, 2012). The foliar N content and GEP_{max} have usually been found to be positively and linearly
12 related in grasses (e.g. Garnier et al., 1999; Chen et al., 2005) and shrubs (e.g. Wright et al., 2001). Across growth
13 forms, species with larger specific leaf area tend to have higher GEP_{max} -N content slopes than species with smaller
14 specific leaf areas, such as shrubs (Reich et al., 1998). The above arguments support a positive GEP_{max} -N content
15 relation. In such a relation, an increase in N availability raises the investment in photosynthetic N use in vascular
16 plants (Hikosaka, 2004) and in *Sphagnum* mosses with low N content (Granath et al., 2009a).

17
18 In contrast, in long-term N fertilization experiments (8-15-year N amendments) a decoupling of GEP_{max} and foliar N
19 has been observed in a red pine forest (Bauer et al., 2004), and more importantly in the ericaceous shrubs at the Mer
20 Bleue Bog (Bubier et al., 2011). Bubier et al. (2011) argued that these long-lived shrubs are adapted to a low-N
21 environment and they allocated N to growth, yet with no changes in the photosynthetic rates. This finding was in line
22 with the reported maintenance of metabolic homeostasis in *Carex* and *Eriophorum* under increased nutrient
23 availability in Arctic tundra (Shaver and Laundre, 1997). Similarly, photosynthesis of *Calluna* was found to be
24 unaffected by experimentally added N (Whitehead et al., 1997; Currey et al., 2011). This finding was attributed to
25 the slow growth rates and N use priorities of *Calluna*. Although a large increase in graminoid biomass was not found
26 after 9 years of fertilization in the NPK plots of the Mer Bleue Bog, the observed limitation of GEP_{max} to benefit
27 from high N content in shrubs indicated a lesser competitive advantage of shrubs compared to other PFTs, including
28 graminoids (Bubier et al., 2011).

29
30 To examine the importance of such empirical findings, we modified the GEP_{max} -N relation of shrubs (Fig. 8b,
31 Appendix A and B, Modification 1) according to the observed lack of relation within the leaf N content range of 1.5
32 and 2.5 g m^{-2} (Bubier et al., 2011), equivalent to 0.03 to 0.05 g N g C^{-1} in the model. None of the modifications
33 improved model performance in all aspects. Modification 1 resulted in a better fit of the modeled GEP during the
34 first 5 years of fertilization in 20NPK (Fig. 8a). On the other hand, mosses did not decline as much in the long-term
35 simulation as they did on the fertilization plots (Fig. 8f). This effect was due to less shading from vascular plants in
36 the model. Alternatively, modifying both the GEP_{max} -N relations of shrubs and graminoids (Modification 2, 3) (Fig.
37 8c, 8d) greatly reduced the discrepancies between the simulated and observed GEP and NEE (Fig. 9a). Also in these
38 modifications, mosses did not decline, but graminoids did not increase either, as was also observed with respect to
39 the graminoids in the field. In both Modification 2 and 3, the GEP_{max} of graminoids decreases with leaf N content
40 above 2 g N m^{-2} , equivalent to $0.024\text{ g N g C}^{-1}$ (Fig. 8c, 8d). The biggest improvement of model performance
41 regarding C fluxes occurred with Modification 3, in which GEP_{max} in both graminoids and shrubs strongly decrease
42 with N content in shoots above their optimal N contents (Fig. 8d). This modification was not realistic if we compare
43 it with the observations, i.e. a lack of clear trend in the leaf photosynthetic capacity with leaf N content, more
44 deciduous shrub biomass in the NPK fertilized plots (Bubier et al., 2011), and a different type of vegetation in the
45 model and in the experimental area. However, it shows that the original model with its positive GEP_{max} - N relation
46 in shrubs was not able to capture the observed kind of ecosystem trajectory.

47
48 The improvement in simulations with non-linear dependency of GEP_{max} to N content suggested that the relationship
49 between GEP_{max} and N in all PFTs follows a unimodal model. This interpretation includes the graminoids, which
50 were earlier characterized by a linear dependency of GEP_{max} on N content (Sage and Percy, 1987; Garnier et al.,

1 1999). Although there have been reports of a threshold N content for photosynthesis in graminoids, growth of a
2 graminoid (*Eriophorum vaginatum*) was not affected, while photosynthesis accelerated after 5 years of N amendment
3 at 5.6 g N m⁻² yr⁻¹ (Currey et al., 2011). Similarly, graminoids were found maintaining their metabolic homeostasis
4 while accumulating more biomass after 2 years of fertilization at 10 g N m⁻² yr⁻¹ and 5 gP m⁻² yr⁻¹ in an Arctic tundra
5 (Shaver and Laundre, 1997). Currey et al. (2011) suggested that additional investment in root growth or storage of
6 the assimilated C contributed to the decoupling of aboveground growth and photosynthesis (Currey et al., 2011). Our
7 results support this argument, as increases in the root/shoot growth ratio and photosynthesis rate were simulated, if
8 only during the first 3 years (Fig. S1a). Using Modification 3, increases in the growth in graminoid roots and GEP
9 were not sustained due to the limited photosynthesis (Fig. S1b), and ultimately led to a complete decline of
10 graminoids (Fig. 8h). Indeed, increases in the biomass of graminoids have not been observed at the N fertilization
11 plots of the Mer Bleue Bog to date. *Eriophorum vaginatum* is a common graminoid at Mer Bleue, but it is more
12 abundant on the moister areas of the bog and scarce at the location of the fertilization experiment, where only
13 scattered individuals occur. The GEP_{max} of graminoids in the fertilization plots would need to be further examined in
14 order to certify whether an N content threshold exists for photosynthetic capacity in graminoids. In addition, other
15 feedbacks may have affected the plant competition and should be considered to improve model predictions. For
16 example, the recently observed increase in the water table level in 20NPK may facilitate the expansion of graminoids
17 in the future (Larmola et al. 2013), while the increase of the water table level was negligible in the current model.

18 **3.6 The importance of time scale for the effect of N deposition on C fluxes**

19
20 The simulated annual GEP, ER and NEE showed large variations among the varied GEP_{max}-N relations in the first
21 years and separated into two groups after 20 years of fertilization (Fig. 9d-9f). The results showed a continuing
22 positive effect of long-term N deposition on the NEE of the graminoid-dominated system, whereas a release of C
23 from the peatland occurred in the shrub-moss dominated scenarios. The changes in the C fluxes in the first few years
24 were not indicative of the long-term changes in C fluxes, which started to emerge after 10 years. The original
25 simulation and the Modification 1 simulation predicted a shift of the PFTs from shrub-moss dominated to graminoid-
26 dominated. This path turned the bog into a large C sink after 20 years of fertilization in the simulated 20NPK
27 treatment at a deposition of 6.4 g N m⁻² yr⁻¹. In contrast, in simulations with Modifications 2 and 3 the bog remained
28 shrub-moss dominated and switched to a small C source after 20 years of fertilization in the same treatment (Fig. 9d-
29 9f). In the graminoid-dominated scenarios the peatland contained a much higher total aboveground biomass, and had
30 a significantly higher GEP, ER and NEE than in the shrub-moss dominated type.

31
32 Previous work has also suggested occurrence of alternative stable states in peatlands. Using an analytical modeling
33 approach, Hilbert et al. (2000) identified two stable ecological states of peatlands, resembling either wet fens with
34 thinner peat and dry bogs with thicker peat. In contrast to these states, our simulation suggested a higher productivity
35 and peat accumulation in the graminoid-dominated than the shrub-dominated system. A promotion of plant
36 productivity by N deposition, within their tolerance range, was not considered by Hilbert and colleagues' model,
37 which simulated a limited primary production in fens (Hilbert et al., 2000). A dichotomy in vegetation community
38 composition was also predicted by an N-sensitive *Sphagnum*-vascular competition model (Pastor et al., 2001). The
39 authors showed a strong dependence of the equilibrium size of plants regarding their competition for nutrients, as
40 was also the case in our simulations (Fig. 8 - 9).

41
42 On the ecosystem scale, other processes beyond those simulated need to be considered. For example, further PFTs, in
43 particular trees, herbs or deciduous shrubs, might benefit from N enrichment and become important in the
44 competition among plants for resources (Tomassen et al., 2003; Huotari et al., 2008). Accordingly ferns and birch
45 have become more prevalent at the 6.4 g N m⁻² yr⁻¹ (PK) fertilization level in the Mer Bleue bog (Larmola et al. 2013;
46 personal observation). Moreover, competition among species within a PFT could either reinforce or abate the
47 competitive differences among PFTs through replacing less tolerant species by those that are more adapted to the
48 changing environment (e.g. Mulligan and Gignac, 2002; Rydin, 1993). The model does not consider interspecies
49 competition within a PFT and thus likely overestimated competitive exclusion among PFTs (Gunnarsson et al., 2004;

1 Robroek et al., 2009). For example, species composition had not significantly changed during the study period,
2 whereas the abundance of species has been altered dramatically by long-term atmospheric N deposition in a Czech
3 mountain bog (Hájková et al., 2011). Interspecies competition is also related to environmental factors, such as soil
4 moisture and temperature, that affect the sensitivity of PFTs to N deposition and lead to site-specific responses of
5 vegetation to N deposition (Clark et al., 2007; Limpens et al., 2011; Gunnarsson and Flodin, 2007). For example,
6 *Chamaedaphne calyculata*, which favors dry conditions and is tolerant to a wider range of water table depth than
7 *Ledum groenlandicum* (Bubier et al., 2006), showed greater increases in the biomass than the latter with N
8 fertilization (Bubier et al., 2011). Also, the production of *Sphagnum* biomass was more sensitive to N deposition at
9 sites with higher July temperature and higher annual precipitation (Limpens et al., 2011).

10
11 In our model, the changes in the vegetation biomass and composition induced by N deposition were determined by
12 the capability of PFTs to benefit from additionally available N. This capability included the ability to uptake N, the
13 response of GEP_{max} to N content, and the fate of the assimilated C in maximizing nutrient uptake, light absorption,
14 and plant growth. Due to the lack of empirical data that address the above issues, large uncertainties about potential
15 shifts in the vegetation community composition remain. Therefore it is essential to identify the adaptation and growth
16 strategies of bog species to the nutrient poor environment in predicting the competition among PFTs. To do so is a
17 prerequisite for more accurately predicting the path the system will follow in the long-term under conditions of
18 potential competitive exclusion of PFTs. The final plant composition and biomass in the evolving ecosystem are
19 essential for predicting the effect of N deposition on C cycling in the long-term, as suggested by our modeling results.

23 4. Conclusions

24
25 The PEATBOG model, version 1.1, does not consider nutritional limitations other than by N and this way represents
26 a situation as empirically induced by the NPK fertilization scheme that was modeled. Other evidence has shown that
27 productivity in the Mer Bleue peatland is likely NP co-limited so that effects of N deposition alone would likely be
28 different from those measured and modeled (Wang et al., 2013; Wang and Moore, 2014; Larmola et al., 2013). The
29 legitimacy of extrapolating our results to atmospheric N deposition is thus limited and caution should be exercised in
30 generalizing the results.

31
32 Acknowledging such reservations, the study demonstrated the ability of the PEATBOG model to correctly reproduce
33 the magnitude of C fluxes under ambient conditions and with increased N deposition levels. The model output
34 deviated from field measurements in its slower decline of moss productivity and biomass and a more rapid increase
35 in GEP with N fertilization. Simulations over 80 years predicted an acceleration of C cycling and greatly enhanced
36 GEP, ER and NEE at higher N deposition levels. The effect of N deposition was closely related to changes in the
37 distribution between the plant functional types and the plant biomass after about 15 years had passed. The response
38 of the C fluxes to elevated N input differed between the plants and the soil. The model results documented an
39 instantaneous increase in the primary production, autotrophic respiration and litter production after N fertilization
40 began. In contrast a delay of 10 to 15 years occurred with regard to the increase in heterotrophic respiration and CH₄
41 emission. Large changes in C fluxes only occurred during the first 20 years of fertilization. Afterwards, C fluxes
42 were predominantly constrained by the vegetation composition and biomass in the new system. From this finding
43 one may conclude that the short-term experiments that we conducted may not easily be extrapolated to longer time
44 periods.

45
46 The original model parameterization resulted in a considerable discrepancy between the short-term simulated and
47 observed GEP. This discrepancy was diminished by modifying the response of photosynthetic capacity to the N
48 content in vascular plants from linear to unimodal. However, unimodal relations with photosynthetic capacity of

1 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
 2 inhibition from vascular plants on the growth of mosses and maintained the presence of mosses even at the highest
 3 fertilization level. With linear or unimodal photosynthetic capacity - N content relation applied on vascular plants,
 4 the carbon fluxes deviated along two possible paths that were characterized by dominance of different PFT, similar
 5 to the trajectories that were simulated by analytical models on peatland ecosystem equilibria (Hilbert et al., 2000;
 6 Pastor et al., 2002). A graminoid-dominated peatland evolved that was characterized by high GEP, ER and NEE.
 7 Alternatively the peatland remained shrub-moss dominated and had smaller GEP, ER and NEE. In the sedge-
 8 dominant peatland type, a shift from C gain to C loss was predicted by the model after about 700 years of
 9 fertilization and at the highest N fertilization level only. In contrast, in the shrub-moss dominated peatland type, a net
 10 C loss occurred already within 20 years. The model emphasizes the importance of vegetation dynamics for C fluxes
 11 in northern peatlands. This finding is, in our view, the most crucial outcome of the modeling analysis: The vegetation
 12 dynamics responds non-linearly to environmental controls and may show different stable states under otherwise
 13 similar conditions that will lead to very different outcomes in terms of carbon fluxes and sequestration. More
 14 empirical information is thus needed regarding the competition among PFTs and the benefits individual plant
 15 functional types may receive from changes in N availability, for example through increasing photosynthetic capacity.
 16
 17

18 Acknowledgements

19
 20 We greatly acknowledge useful discussions with J. Verhoeven, N. Dise, B. Svensson, B. Robroek, L. Bragazza and P. E. Lindgren
 21 that helped clarify concepts in the model development. We further thank P. Lafleur, N. T. Roulet and E. R. Humphreys for
 22 facilitating access to data related to the Mer Bleue Peatland and two referees for their insightful comments. This study is part of
 23 the BiodivERsA-PeatBOG project whose German subproject was funded by the German Ministry of Education and Research
 24 (BMBF) grant 01LC0819A to C. Blodau through ERA-net (European Union's 6th Framework). We would like to extend thanks to
 25 the Natural Sciences and Engineering Research Council (NSERC) Discovery Grant to T. Moore, the Ontario Early Researcher
 26 Award to C. Blodau and the National Science Foundation grants DEB-0346625 and DEB-1019523 to J. L. Bubier, S. Jutinen
 27 and T. Larmola. Y. Wu was supported by a Ph.D. fellowship of the University of Münster.
 28

29 Appendix A: Equations in PEATBOG 1.1.

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

$$31 \quad fN_{GEP} = \begin{cases} 0 & \text{if } 0 \leq N_{leaf} < N_{min} \\ aN_{leaf} - b & \text{if } N_{min} \leq N_{leaf} < N_{opt} \\ 1 & \text{if } N_{opt} \leq N_{leaf} \end{cases} \quad \text{Eqn. 1}$$

32 N_{leaf} is the N content in the leaf of each PFT (gN m^{-2})

33 The parameter a indicates the sensitivity of GEP_{\max} to the leaf N content, and is assigned to 1.00 for graminoids and
 34 0.65 for shrubs. The parameter b indicates the minimum leaf N content for GEP_{\max} and is assigned to -0.60 for
 35 graminoids and -0.30 for shrubs. The parameter values are estimated from Figure 1 in Hikosaka (et al., 2004).
 36

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

$$38 \quad fN_{GEP} = \begin{cases} 0 & \text{if } 0 \leq N_{foliar} < N_{min} \\ 1 - \tanh(\alpha_1(N_{opt} - N_{foliar})/N_{opt})^{\beta_1} & \text{if } N_{min} \leq N_{foliar} < N_{opt} \\ 1 - \tanh(\alpha_2(N_{foliar} - N_{opt})/N_{opt})^{\beta_2} & \text{if } N_{opt} \leq N_{foliar} < N_{max} \\ 0 & \text{if } N_{max} \leq N_{foliar} \end{cases} \quad \text{Eqn. 2}$$

39 The parameters α and β determine the sensitivity of the photosynthetic capacity (GEP_{\max}) to the N content in leaves
 40 (N_{foliar}). Large values of α indicate low GEP_{\max} and low N- GEP_{\max} gradient approaching the minimum and the

1 maximum N content (N_{\min} and N_{\max}). Large values of β indicate low N-GEP_{max} gradient approaching the optimal N
 2 content (N_{opt}). For example, α_2 and β_2 for graminoids in Modification 3 are larger than that in Modification 2m
 3 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
 4 photosynthesis are lower in the shrubs than in the graminoids, considering that shrubs are more limited to N and
 5 more conservative in their N cycling. The values of the parameters in equation 2 are listed in Appendix 2.

6
 7 3. Ecosystem respiration (ER)

$$8 \quad ER = \sum_{j=1}^3 (Rm_{X,j} + Rg_{X,j}) + \sum_{i=1}^{20} Rh_{q,i} \quad \text{Eqn. 3}$$

9 ER ($\text{gC m}^{-2} \text{day}^{-1}$) is aggregated from the maintenance respiration (Rm) and growth respiration (Rg) of all C pools in
 10 leaf, stem and root of the plants (X) and the heterotrophic respiration (Rh) of the labile and recalcitrant C pool (q) in
 11 the soil layers (j).

$$12 \quad Rm_{X,j} = rm_{X,j} C_{\text{struc},X,j} fm_{X,j} fT_{X,j} \quad \text{Eqn. 4}$$

$$13 \quad Rg_{X,j} = rg_{X,j} C_{\text{struc},X,j} fm_{X,j} fT_{X,j} \frac{C_{\text{subs},X,j}}{C_{\text{subs},X,j} + kC_{g,j}} \frac{N_{\text{subs},X,j}}{N_{\text{subs},X,j} + kN_{g,j}} (1 - k_{g,j}) / k_{g,j} \quad \text{Eqn. 5}$$

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

$$19 \quad Rh_{q,i} = C_{q,i} k_{\text{pot},q,i} fT_{\text{dec},q,i} fm_{\text{dec},q,i} f_{N,i} f_{\text{inhib},i} \left(\frac{1}{CN_{q,i}} - \frac{1}{CN_{\text{crit},q,i}} \right) \quad \text{Eqn. 6}$$

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

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

27
 28 4. The competition for N uptake by PFTs

$$29 \quad Nu_{pt,j} = \sum_i^{\text{root}} \sum_k^3 Nu_{pt,i,k} \quad \text{Eqn. 7}$$

$$30 \quad Nu_{pt,i,k} = \frac{V_{j,k} N_{\text{conc},i,j}}{k_{j,k} + N_{\text{conc},i,j}} fC_{rt,i,j} fT Nu_{pt,i,j} / \left(1 + \frac{kC_{upt,j}}{C_{rt,subs,j}} \left(1 + \frac{N_{rt,subs,j}}{kNu_{pt,j}} \right) \right) \quad \text{Eqn. 8}$$

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

33 The N uptake rates of each layer of each PFT is obtained using the Michaelis-Menten function with PFT-specific
 34 uptake capacity ($V_{j,k}$) and half saturation constant ($k_{j,k}$) and the dynamical layer-specific N concentrations ($N_{\text{conc},i,j}$).

1 The uptake rates are modified by the biomass or area of the fine roots ($fCr_{t,i,j}$), a temperature factor ($fTN_{upt,i,j}$), the
 2 substrate C and N concentrations in the roots ($Cr_{tsub,j}$, $Nr_{tsub,j}$), and the PFT-specific parameters kC_{uptj} and kN_{uptj} .

3
 4 **Appendix B: Parameter values of GEPmax as hyperbolic functions of foliar N content (N_{foliar})**

Parameter	Description	Graminoids	Graminoids	Shrubs
		Modification 2	Modification 3	Modification 1 to 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

5

6 **References**

7
 8 Aaby, B.: Monitoring Danish raised bogs, mires and man: Mire conservation in a densely populated country: The
 9 Swiss experience, edited by: Gruenig, A., Swiss Federal Institute for Forest, Snow and Landscape Research,
 10 Birmensdorf, Switzerland, 284-300 pp., 1994.
 11 Aerts, R., Decaluwe, H., and Konings, H.: Seasonal allocation of biomass and nitrogen in 4 *Carex* species from
 12 mesotrophic and eutrophic fens as affected by nitrogen supply, *Journal of Ecology*, 80, 653-664,
 13 10.2307/2260857, 1992.
 14 Aerts, R., J. T. A. Verhoeven, and D. F. Whigham: plant-mediated controls on nutrient cycling in temperate fens and
 15 bogs, *Ecology*, 80, 2170–2181, doi:10.2307/176901, 1999.
 16 Aerts, R., Wallén, B., Malmer, N., and De Caluwe, H.: Nutritional constraints on *Sphagnum*-growth and potential
 17 decay in northern peatlands, *Journal of Ecology*, 89, 292-299, 2001.
 18 Aerts, R., van Logtestijn, R. S., and Karlsson, P. S.: Nitrogen supply differentially affects litter decomposition rates
 19 and nitrogen dynamics of sub-arctic bog species, *Oecologia*, 146, 652-658, 10.1007/s00442-005-0247-5, 2006.
 20 Bauer, G. A., Bazzaz, F. A., Minocha, R., Long, S., Magill, A., Aber, J., and Berntson, G. M.: Effects of chronic N
 21 additions on tissue chemistry, photosynthetic capacity, and carbon sequestration potential of a red pine (*Pinus*
 22 *resinosa* Ait.) stand in the NE United States, *Forest Ecology and Management*, 196, 173-186,
 23 10.1016/j.foreco.2004.03.032, 2004.
 24 Blodau, C., and Moore, T. R.: Macroporosity affects water movement and pore water sampling in peat soils, *Soil*
 25 *Science*, 167, 98-109, 2002.
 26 Bragazza, L., Limpens, J., Gerdol, R., Grosvernier, P., Hajek, M., Hájek, T., Hajkova P., Hansen. I., Iacumin, P.,
 27 Kutnar, L., Rydin, H. and Tahvanainess, T.: Nitrogen concentration and $\delta^{15}N$ signature of ombrotrophic
 28 *Sphagnum* mosses at different N deposition levels in Europe, *Global Change Biology* 11(1), 106-114, 2005.
 29 Bragazza, L., Freeman, C., Jones, T., Rydin, H., Limpens, J., Fenner, N., Ellis, T., Gerdol, R., Hajek, M., Hajek, T.,
 30 Iacumin, P., Kutnar, L., Tahvanainen, T., and Toberman, H.: Atmospheric nitrogen deposition promotes carbon
 31 loss from peat bogs, *Proceedings of the National Academy of Sciences of the United States of America*, 103,
 32 19386-19389, 10.1073/pnas.0606629104, 2006.
 33 Bragazza, L., and Freeman, C.: High nitrogen availability reduces polyphenol content in *Sphagnum* peat, *The*
 34 *Science of the Total Environment*, 377, 439-443, 10.1016/j.scitotenv.2007.02.016, 2007.

- 1 Bragazza, L., Siffi, C., Iacumin, P., and Gerdol, R.: Mass loss and nutrient release during litter decay in peatland:
2 The role of microbial adaptability to litter chemistry, *Soil Biology and Biochemistry*, 39, 257-267,
3 10.1016/j.soilbio.2006.07.014, 2007.
- 4 Bragazza, L., Buttler, A., Siegenthaler, A., and Mitchell, E. A. D.: Plant litter decomposition and nutrient release in
5 peatlands, *Geophysical Monograph Series*, 184, 99-110, 2009.
- 6 Bragazza, L., Buttler, A., Habermacher, J., Brancaleoni, L., Gerdol, R., Fritze, H., Hanajík, P., Laiho, R., and
7 Johnson, D.: High nitrogen deposition alters the decomposition of bog plant litter and reduces carbon
8 accumulation, *Global Change Biology*, 18, 1163-1172, 10.1111/j.1365-2486.2011.02585.x, 2012.
- 9 Breeuwer, A., Heijmans, M., Robroek, B. J. M., Limpens, J., and Berendse, F.: The effect of increased temperature
10 and nitrogen deposition on decomposition in bogs, *Oikos*, 117, 1258-1268, 2008.
- 11 Bubier, J. L., Bhatia, G., Moore, T. R., Roulet, N. T., and Lafleur, P. M.: Spatial and temporal variability in growing-
12 season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada, *Ecosystems*, 6, 353-367,
13 2003.
- 14 Bubier, J. L., Moore, T. R., and Bledzki, L. A.: Effects of nutrient addition on vegetation and carbon cycling in an
15 ombrotrophic bog, *Global Change Biology*, 13, 1168-1186, 10.1111/j.1365-2486.2007.01346.x, 2007.
- 16 Bubier, J. L., Moore, T. R., and Crosby, G. Fine-scale vegetation distribution in a cool temperate bog, *Canadian
17 Journal of Botany*, 84, 910-923, 2006.
- 18 Bubier, J. L., Smith, R., Juutinen, S., Moore, T. R., Minocha, R., Long, S., and Minocha, S.: Effects of nutrient
19 addition on leaf chemistry, morphology, and photosynthetic capacity of three bog shrubs, *Oecologia*, 167, 355-
20 368, 10.1007/s00442-011-1998-9, 2011.
- 21 Chapin III, F. and Shaver, G. R.: Differences in growth and nutrient use among arctic plant growth forms, *Functional
22 Ecology*, 3(1), 73-80, 1989.
- 23 Chen, S., Bai, Y., Zhang, L., and Han, X.: Comparing physiological responses of two dominant grass species to
24 nitrogen addition in Xilin River Basin of China, *Environmental and Experimental Botany*, 53, 65-75, 2005.
- 25 Chong, M., Humphreys, E.R. and Moore, T.R.: Microclimatic response to increasing shrub cover and its effect on
26 *Sphagnum* CO₂ exchange in a bog. *Ecoscience*, 19: 89-97, 2012.
- 27 Clark, C. M., Cleland, E. E., Collins, S. L., Fargione, J. E., Gough, L., Gross, K. L., Pennings, S. C., Suding, K. N.,
28 and Grace, J. B.: Environmental and plant community determinants of species loss following nitrogen
29 enrichment, *Ecology Letters*, 10, 596-607, 10.1111/j.1461-0248.2007.01053.x, 2007.
- 30 Currey, P. M., Johnson, D., Dawson, L. A., van der Wal, R., Thornton, B., Sheppard, L. J., Leith, I. D., and Artz, R.
31 R. E.: Five years of simulated atmospheric nitrogen deposition have only subtle effects on the fate of newly
32 synthesized carbon in *Calluna vulgaris* and *Eriophorum vaginatum*, *Soil Biology and Biochemistry*, 43, 495-
33 502, 10.1016/j.soilbio.2010.11.003, 2011.
- 34 Evans, J. R.: Photosynthesis and nitrogen relationships in leaves of C₃ plants, *Oecologia*, 78, 9-19, doi:
35 10.1007/BF00377192, 1989.
- 36 Garnier, E., Salager, J. L., Laurent, G., and Sonié, L.: Relationships between photosynthesis, nitrogen and leaf
37 structure in 14 grass species and their dependence on the basis of expression, *New Phytologist*, 143, 119-129,
38 10.2307/2588520, 1999.
- 39 Gerdol, R., Bragazza, L., and Brancaleoni, L.: Heatwave 2003: high summer temperature, rather than experimental
40 fertilization, affects vegetation and CO₂ exchange in an alpine bog, *The New Phytologist*, 179, 142-154,
41 10.1111/j.1469-8137.2008.02429.x, 2008.
- 42 Granath, G., Strengbom, J., Breeuwer, A., Heijmans, M. M., Berendse, F., and Rydin, H.: Photosynthetic
43 performance in *Sphagnum* transplanted along a latitudinal nitrogen deposition gradient, *Oecologia*, 159, 705-
44 715, 10.1007/s00442-008-1261-1, 2009a.
- 45 Granath, G., Wiedermann M. M., and Strengbom J.: Physiological responses to nitrogen and sulphur addition and
46 raised temperature in *Sphagnum balticum*, *Oecologia* 161, 481-490, doi: 10.1007/s00442-009-1406-x, 2009b.
- 47 Granath, G., Strengbom, J. and Rydin, H.: Direct physiological effects of nitrogen on *Sphagnum*: a greenhouse
48 experiment. *Functional Ecology*, 26, 353-364, doi: 10.1111/j.1365-2435.2011.01948.x, 2012.
- 49 Granberg, G., Grip, H., Löfvenius, M. O., Sundh, I., Svensson, B., and Nilsson, M.: A simple model for simulation
50 of water content, soil frost, and soil temperatures in boreal mixed mires, *Water Resources Research*, 35, 3771-

- 1 3782, 1999.
- 2 Greven, H. C.: Changes in the moss flora of the Netherlands, *Biological Conservation*, 59, 133-137, 10.1016/0006-
3 3207(92)90572-5, 1992.
- 4 Gunnarsson, U., Granberg, G., and Nilsson, M.: Growth, production and interspecific competition in *Sphagnum*:
5 effects of temperature, nitrogen and sulphur treatments on a boreal mire, *New Phytologist*, 163, 349-359, 2004.
- 6 Gunnarsson, U., and Flodin, L. A.: Vegetation shifts towards wetter site conditions on oceanic ombrotrophic bogs in
7 southwestern Sweden, *Journal of Vegetation Science*, 18, 595-604, 10.1111/j.1654-1103.2007.tb02573.x, 2007.
- 8 Hájková, P., Hájek, M., Rybníček, K., Jiroušek, M., Tichý, L., Králová, Š., and Mikulášková, E.: Long-term
9 vegetation changes in bogs exposed to high atmospheric deposition, aerial liming and climate fluctuation,
10 *Journal of Vegetation Science*, 22, 891-904, 2011.
- 11 Heijmans, M. M. P. D., Berendse, F., Arp, W. J., Masselink, A. K., Klees, H., De Visser, W., and Van Breemen, N.:
12 Effects of elevated carbon dioxide and increased nitrogen deposition on bog vegetation in the Netherlands,
13 *Journal of Ecology*, 89, 268-279, 2001.
- 14 Heijmans, M. M. P. D., Mauquoy, D., Geel, B., and Berendse, F.: Long-term effects of climate change on vegetation
15 and carbon dynamics in peat bogs, *Journal of Vegetation Science*, 19(3), 307-320, doi: 10.3170/2008-8-18368,
16 2008.
- 17 Hikosaka, K.: Interspecific difference in the photosynthesis-nitrogen relationship: patterns, physiological causes, and
18 ecological importance, *Journal of Plant Research*, 117, 481-494, 10.1007/s10265-004-0174-2, 2004.
- 19 Hikosaka, K., and I. Terashima.: A model of the acclimation of photosynthesis in the leaves of C3 plants to sun and
20 shade with respect to nitrogen use, *Plant, Cell & Environment*, 18, 605-618, doi: 10.1111/j.1365-
21 3040.1995.tb00562.x, 1995.
- 22 Hilbert, D.W., Roulet N.T. and Moore T.R.: Modelling and analysis of peatlands as dynamic systems. *Journal of*
23 *Ecology* 88: 241-256, 2000.
- 24 Huotari, N., Tillman-Sutela, E., Pasanen, J., and Kubin, E.: Ash-fertilization improves germination and early
25 establishment of birch (*Betula pubescens Ehrh.*) seedlings on a cut-away peatland, *Forest Ecology and*
26 *Management*, 255, 2870-2875, <http://dx.doi.org/10.1016/j.foreco.2008.01.062>, 2008.
- 27 Juutinen, S., Bubier, J. L., and Moore, T. R.: Responses of vegetation and ecosystem CO₂ exchange to 9 Years of
28 nutrient addition at Mer Bleue Bog, *Ecosystems*, 13, 874-887, 10.1007/s10021-010-9361-2, 2010.
- 29 Kimball, J. S., Thornton, P. E., White, M. A., and Running, S. W.: Simulating forest productivity and surface-
30 atmosphere carbon exchange in the BOREAS study region, *Tree Physiology*, 17 (8-9), 589-599, 1997.
- 31 Kirk, G. J. D., and Kronzucker H. J.: The potential for nitrification and nitrate uptake in the rhizosphere of wetland
32 plants: a modelling study, *Annals of Botany*, 96 (4), 639-646, 2005.
- 33 Knapp, A. K., and Smith, M. D.: Variation among biomes in temporal dynamics of aboveground primary production,
34 *Science*, 291, 481-484, 2001.
- 35 Knorr, M., Frey, S. D., and Curtis, P. S.: Nitrogen additions and litter decomposition: A meta-analysis, *Ecology*, 86,
36 3252-3257, 10.1890/05-0150, 2005.
- 37 Lafleur, P. M., Roulet, N. T., Bubier, J. L., Frolking, S., and Moore T. R.: Interannual variability in the peatland-
38 atmosphere carbon dioxide exchange at an ombrotrophic bog, *Global Biogeochemical Cycles*, 17, 1036,
39 doi:10.1029/2002GB001983, 2, 2003.
- 40 Laine, A. M., Bubier, J., Riutta, T., Nilsson, M. B., Moore, T. R., Vasander, H., and Tuittila, E. S.: Abundance and
41 composition of plant biomass as potential controls for mire net ecosystem CO₂ exchange, *Botany*, 90, 63-74,
42 10.1139/b11-068, 2012.
- 43 Lamarque, J. R. , G. P. Kyle, M. Meinshausen, K. Riahi, S. J. Smith, D. P. Vuuren, A. J. Conley, and F. Vitt.: Global
44 and regional evolution of short-lived radiatively-active gases and aerosols in the representative concentration
45 pathways." *Climatic Change* 109 (1-2): 191–212. doi:10.1007/s10584011-0155-0, 2011.
- 46 Lang, S. I., Cornelissen, J. H. C., Klahn, T., van Logtestijn, R. S. P., Broekman, R., Schweikert, W., and Aerts, R.:
47 An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic
48 bryophyte, lichen and vascular plant species, *Journal of Ecology*, 97, 886-900, 10.1111/j.1365-
49 2745.2009.01538.x, 2009.
- 50 Larmola, T., Bubier, J. L., Kobylyanec, C., Basiliko, N., Juutinen, S., Humphreys, E., Preston, M., and Moore, T. R.:

- 1 Vegetation feedbacks of nutrient addition lead to a weaker carbon sink in an ombrotrophic bog, *Global Change*
2 *Biology*, 19, 3729-3739, 2013.
- 3 LeBauer, D. S., and Treseder, K. K.: Nitrogen limitation of net primary productivity in terrestrial ecosystems is
4 globally distributed, *Ecology*, 89, 371-379, 2008.
- 5 Limpens, J., and Berendse, F.: How litter quality affects mass loss and N loss from decomposing *Sphagnum*, *Oikos*,
6 103, 537-547, 10.1034/j.1600-0706.2003.12707.x, 2003.
- 7 Limpens, J., Granath, G., Gunnarsson, U., Aerts, R., Bayley, S., Bragazza, L., Bubier, J., Buttler, A., van den Berg, L.
8 J., Francez, A. J., Gerdol, R., Grosvernier, P., Heijmans, M. M., Hoosbeek, M. R., Hotes, S., Ilomets, M., Leith,
9 I., Mitchell, E. A., Moore, T., Nilsson, M. B., Nordbakken, J. F., Rochefort, L., Rydin, H., Sheppard, L. J.,
10 Thormann, M., Wiedermann, M. M., Williams, B. L., and Xu, B.: Climatic modifiers of the response to
11 nitrogen deposition in peat-forming *Sphagnum* mosses: a meta-analysis, *The New Phytologist*, 191, 496-507,
12 10.1111/j.1469-8137.2011.03680.x, 2011.
- 13 Liu, L. L., and Greaver, T. L.: A global perspective on belowground carbon dynamics under nitrogen enrichment,
14 *Ecology Letters*, 13, 819-828, 10.1111/j.1461-0248.2010.01482.x, 2010.
- 15 Loisel, J., Z. Yu, D.W. Beilman, P. Camill, J. Alm, M.J. Amesbury, D. Anderson, S. Andersson, C. Bochicchio, K.
16 Barber, L.R. Belyea, J. Bunbury, F. M. Chambers, D.J. Charman, F. De Vleeschouwer, B. Fialkiewicz-Kozielec,
17 S.A. Finkelstein, M. Gałka, M. Garneau, D. Hammarlund, W. Hinchcliffe, J. Holmquist, P. Hughes, M.C.
18 Jones, E.S. Klein, U. Kokfelt, A. Korhola, P. Kuhry, A. Lamarre, M. Lamentowicz, D. Large, M. Lavoie, G.
19 MacDonald, G. Magnan, M. Makila, G. Mallon, P. Mathijssen, D. Mauquoy, J. McCarroll, T.R. Moore, J.
20 Nichols, B. O'Reilly, P. Oksanen, M. Packalen, D. Peteet, P.J.H. Richard, S. Robinson, T. Ronkainen, M.
21 Rundgren, A. Britta, K. Sannel, C. Tarnocai, T. Thom, E.-S. Tuittila, M. Turetsky, M. Valiranta, M. van der
22 Linden, B. van Geel, S. van Bellen, D. Vitt, Y. Zhao and W. Zhou: A database and synthesis of northern
23 peatland soil properties and Holocene carbon and nitrogen accumulation. *The Holocene*, in press.
- 24 Lund, M., Lafleur, P. M., Roulet, N. T., Lindroth, A., Christensen, T. R., Aurela, M., Chojnicki, B. H., Flanagan, L.
25 B., Humphreys, E. R., Laurila, T., Oechel, W. C., Olejnik, J., Rinne, J., Schubert, P., and Nilsson, M. B.:
26 Variability in exchange of CO₂ across 12 northern peatland and tundra sites, *Global Change Biology*, 16, 2436-
27 2448, 10.1111/j.1365-2486.2009.02104.x, 2010.
- 28 Mack, M. C., Schuur, E. A. G., Bret-Harte, M. S., Shaver, G. R., and Chapin, F. S.: Ecosystem carbon storage in
29 arctic tundra reduced by long-term nutrient fertilization, *Nature*, 431, 440-443, 10.1038/nature02887, 2004.
- 30 Moore, T., Bubier, J. L., Frolking, S. E., Lafleur, P. M., and Roulet, N. T.: Plant biomass and production and CO₂
31 exchange in an ombrotrophic bog, *Journal of Ecology*, 90, 25-36, 2002.
- 32 Moore, T., Blodau, C., Turunen, J., Roulet, N., and Richard, P. J. H.: Patterns of nitrogen and sulfur accumulation
33 and retention in ombrotrophic bogs, eastern Canada, *Global Change Biology*, 11, 356-367, 2005.
- 34 Moore, T. R., Young, A., Bubier, J. L., Humphreys, E. R., Lafleur, P. M., and Roulet, N. T.: A multi-year record of
35 methane flux at the Mer Bleue Bog, southern Canada, *Ecosystems*, 14, 646-657, 10.1007/s10021-011-9435-9,
36 2011.
- 37 Mulligan, R. C., and Gignac, L. D.: Bryophyte community structure in a boreal poor fen II: interspecific competition
38 among five mosses, *Canadian Journal of Botany*, 80, 330-339, 2002.
- 39 Neff, J. C., Townsend, A. R., Gleixner, G., Lehman, S. J., Turnbull, J., and Bowman, W. D.: Variable effects of
40 nitrogen additions on the stability and turnover of soil carbon, *Nature*, 419, 915-917, 10.1038/nature01136,
41 2002.
- 42 Olsson, P., Linder, S., Giesler, R., and Höglberg, P.: Fertilization of boreal forest reduces both autotrophic and
43 heterotrophic soil respiration, *Global Change Biology*, 11, 1745-1753, 2005.
- 44 Pastor, J., Peckham, B., Bridgman, S., Weltzin, J., and Chen, J.: Plant community dynamics, nutrient cycling, and
45 alternative stable equilibria in peatlands. *The American Naturalist*, 160(5), 553-568, 2002.
- 46 Preston, C. M., Trofymow, J. A. T., and the Canadian Intersite Decomposition Experiment Working Group:
47 Variability in litter quality and its relationship to litter decay in Canadian forests, *Canadian Journal of Botany*,
48 78 (10), 1269-1287, 2000.
- 49 Reich, P., Ellsworth, D., and Walters, M.: Leaf structure (specific leaf area) modulates photosynthesis–nitrogen
50 relations: evidence from within and across species and functional groups, *Functional Ecology*, 12, 948-958,

- 1 1998.
- 2 Reynolds, J. F., and Thornley, J. H. M.: A shoot: root partitioning model, *Annals of Botany*, 49 (5), 585-597, 1982.
- 3 Robroek, B. J., Schouten, M. G., Limpens, J., Berendse, F., and Poorter, H.: Interactive effects of water table and
4 precipitation on net CO₂ assimilation of three co-occurring *Sphagnum* mosses differing in distribution above
5 the water table, *Global Change Biology*, 15, 680-691, 2009.
- 6 Rogora, M., Arisci, S., and Marchetto, A.: The role of nitrogen deposition in the recent nitrate decline in lakes and
7 rivers in Northern Italy, *Science of the Total Environment*, 417, 214-223,
8 <http://dx.doi.org/10.1016/j.scitotenv.2011.12.067>, 2012.
- 9 Roulet, N. T., Lafleur, P. M., Richard, P. J. H., Moore, T. R., Humphreys, E. R., and Bubier, J.: Contemporary
10 carbon balance and late Holocene carbon accumulation in a northern peatland, *Global Change Biology*, 13,
11 397-411, 10.1111/j.1365-2486.2006.01292.x, 2007.
- 12 Rydin, H.: Interspecific competition between *Sphagnum* mosses on a raised bog, *Oikos*, 66 (3), 413-423, 1993.
- 13 Saarinen, T.: Internal C:N balance and biomass partitioning of *Carex rostrata* grown at three levels of nitrogen
14 supply, *Canadian Journal of Botany*, 76, 762-768, 10.1139/b98-046, 1998.
- 15 Sage, R. F., and Pearcy, R. W.: The nitrogen use efficiency of C3 and C4 plants II. Leaf nitrogen effects on the gas
16 exchange characteristics of *Chenopodium album* (L.) and *Amaranthus retroflexus* (L.), *Plant physiology*, 84,
17 959-963, 1987.
- 18 Small, E.: Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog
19 plants, *Can. J. Bot.*, 50, 2227-2233, 1972.
- 20 Spahni, R., Joos, F., Stocker, B. D., Steinacher, M., and Yu, Z. C, Transient simulations of the carbon and nitrogen
21 dynamics in northern peatlands: from the Last Glacial Maximum to the 21st century. *Climate of the Past*, 9,
22 1287-1308, doi:10.5194/cp-9-1287-2013, 2013.
- 23 Taylor, B. R., Prescott, C. E., Parsons, W. F. J., and Parkinson, D.: Substrate control of litter decomposition in four
24 Rocky Mountain coniferous forests. *Canadian Journal of Botany*. 69 (10): 2242-2250, 1991.
- 25 Templer, P. H., Robert W. P., and Goodale C. L.: Effects of nitrogen deposition on greenhouse-gas fluxes for forests
26 and grasslands of North America, *Frontiers in Ecology and the Environment*, 10(10), 547-553,
27 doi:10.1890/120055, 2012.
- 28 Thornley, J. H. M., and Verberne, E. L. J.: A model of nitrogen flows in grassland, *Plant, Cell & Environment*, 12,
29 863-886, 1989.
- 30 Thornley, J. H. M., and Cannell, M. G. R.: Nitrogen relations in a forest plantation—soil organic matter ecosystem
31 model, *Annals of Botany*, 70 (2), 137-151, 1992.
- 32 Thornley, J. H. M., Bergelson, J., and Parsons, A.: Complex dynamics in a carbon-nitrogen model of a grass-legume
33 pasture, *Annals of Botany*, 75, 79-84, 1995.
- 34 Thornley, J. H. M.: *Grassland dynamics: an ecosystem simulation model*, CAB international, 1998.
- 35 Tomassen, H., Smolders, A. J., Lamers, L. P., and Roelofs, J. G.: Stimulated growth of *Betula pubescens* and
36 *Molinia caerulea* on ombrotrophic bogs: role of high levels of atmospheric nitrogen deposition, *Journal of*
37 *Ecology*, 91, 357-370, 2003.
- 38 Townsend, A., Braswell, B., Holland, E., and Penner, J.: Spatial and temporal patterns in terrestrial carbon storage
39 due to deposition of fossil fuel nitrogen, *Ecological Applications*, 6, 806-814, 1996.
- 40 Turetsky, M. R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frohling, S., McGuire, A. D., and Tuittila, E. S.: The
41 resilience and functional role of moss in boreal and arctic ecosystems, *New Phytologist*, 196, 49-67, 2012.
- 42 Turunen, J., Roulet, N. T., Moore, T. R. and Richard, P. J. H.: Nitrogen deposition and increased carbon
43 accumulation in ombrotrophic peatlands in eastern Canada, *Global Biogeochemical Cycles*, 18, GB3002, doi:
44 10.1029/2003GB002154, 2004.
- 45 Van Der Heijden, E., Verbeek, S. K., and Kuiper, P. J. C.: Elevated atmospheric CO₂ and increased nitrogen
46 deposition: effects on C and N metabolism and growth of the peat moss *Sphagnum recurvum* P. Beauv. var.
47 *mucronatum* (Russ.) Warnst, *Global Change Biology*, 6, 201-212, 2001.
- 48 Verstraeten, A., Neiryneck, J., Genouw, G., Cools, N., Roskams, P., and Hens, M: Impact of declining atmospheric
49 deposition on forest soil solution chemistry in Flanders, Belgium. *Atmospheric Environment*, 62, 50-63,
50 <http://dx.doi.org/10.1016/j.atmosenv.2012.08.017>, 2012.

- 1 Wang, M., Murphy, M. T., Moore, T. R.: Nutrient resorption of two evergreen shrubs in response to long-term
2 fertilization in a bog, *Oecologia*, 174, 365–377, doi: 10.1007/s00442-013-2784-7, 2013.
- 3 Wang, M. and Moore, T. R.: Carbon, nitrogen, phosphorus, and potassium stoichiometry in an ombrotrophic
4 peatland reflects plant functional type, *Ecosystems*, 17(4), 673-684, doi: 10.1007/s10021-014-9752-x, 2014.
- 5 Wang, M., Murphy, M. T. and Moore, T. R.: Nutrient resorption of two evergreen shrubs in response to long-term
6 fertilization in a bog, *Oecologia*, 174, 365-377, doi:10.1007/s00442-013-2784-7, 2014.
- 7 Ward, S. E., Bardgett, R. D., McNamara, N. P., and Ostle, N. J.: Plant functional group identity influences short-term
8 peatland ecosystem carbon flux: evidence from a plant removal experiment, *Functional Ecology*, 23, 454-462,
9 2009.
- 10 Whitehead, S., Caporn, S., and Press, M.: Effects of elevated CO₂, nitrogen and phosphorus on the growth and
11 photosynthesis of two upland perennials: *Calluna vulgaris* and *Pteridium aquilinum*, *New Phytologist*, 135,
12 201-211, 1997.
- 13 Willmott, C. J.: Some comments on the evaluation of model performance, *Bulletin of the American Meteorological*
14 *Society*, 63, 1309-1369, 1982.
- 15 Wright, I. J., Reich, P., and Westoby, M.: Strategy shifts in leaf physiology, structure and nutrient content between
16 species of high- and low- rainfall and high- and low- nutrient habitats, *Functional Ecology*, 15, 423-434, 2001.
- 17 Wu, Y., and Blodau, C.: PEATBOG: a biogeochemical model for analyzing coupled carbon and nitrogen dynamics
18 in northern peatlands, *Geosci. Model Dev.*, 6, 1173-1207, 10.5194/gmd-6-1173-2013, 2013.
- 19 Xing, Y., Bubier, J., Moore, T., Murphy, M., Basiliko, N., Wendel, S., and Blodau, C.: The fate of ¹⁵N-nitrate in a
20 northern peatland impacted by long-term experimental nitrogen, phosphorus and potassium fertilization,
21 *Biogeochemistry*, 103, 281-296, doi: 10.1007/s10533-010-9463-0, 2010.
- 22 Yu, Z., Beilman D. W., and Jones M. C.: Sensitivity of northern peatland carbon dynamics to Holocene climate
23 change. *Geophysical Monograph Series*, 184, 55-69, 2009.
- 24 Yu, Z., Loisel, J., Brosseau, D. P., Beilman D. W. and Hunt S. J.: Global peatland dynamics since the Last Glacial
25 Maximum, *Geophysical Research Letters.*, 37, L13402, doi: 10.1029/2010GL043584, 2010.
- 26 Zaehle, S., Ciais, P., Friend, A. D. and Prieur, V.: Carbon benefits of anthropogenic reactive nitrogen offset by
27 nitrous oxide emissions, *Nature Geoscience*, 4 (9), 601-605, DOI: 10.1038/NGEO1207, 2011.

28
29
30
31
32

1 **Table 1 Updated parameters in PEATBOG 1.1**

2 M = C, N; q = labile, recalcitrant; Q = substrate, structural, X = shoots, roots, leaves, stems, fine roots, coarse roots,
 3 DM_g = CO₂, CH₄, O₂, DM_s = NH₄⁺, NO₃⁻, DOM; i = layer i, j = Plant functional type j.

4

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
bPNUE	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 _{grow} _{C,j}	Half saturation constant for substrate C in biomass growth	0.05	0.05	0.1	g C g ⁻¹	6
K _m _{grow} _{N,j}	Half saturation constant for substrate N in biomass growth	5	0.3	0.5	g N kg ⁻¹	6
ρ _{C,j}	Resistance parameter for shoot root transport of substrate C	–	60	50	m ² day g ⁻¹	7
k _i _{subs} _N	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 _{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 kCpot _L = 45kCpot _R			day ⁻¹	Calibrated
k _{fix}	Base N ₂ fixation rate	0.001			g N m ⁻² day ⁻¹	12 Calibrated

5
 6 Values are assumed or calibrated based on these references: ¹[Chapin III and Shaver, 1989], ²[Small, 1972], ³[Chapin
 7 III and Shaver, 1989], ⁴[Bragazza et al., 2005], ⁵[Heijmans et al., 2008], ⁶[Thornley et al., 1995], ⁷[Reynolds and
 8 Thornley, 1982], ⁸[Thornley and Cannell, 1992], ⁹[Kimball et al., 1997], ¹⁰[Kirk and Kronzucker, 2005], ¹¹[Moore et al.,
 9 2002], ¹²[Moore et al., 2005].

10

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

GEP								
	Control		5NPK		10NPK		20NPK	
	Modeled	Modeled corrected	Modeled	Modeled corrected	Modeled	Modeled corrected	Modeled	Modeled 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

9

10

1 **Table 3 Simulated and observed soil organic C pool (g C m⁻²) in the upper 10 cm of peat, in**
 2 **mosses, plant stems, leaves, and fine roots of treatments. Also the leaf area index (LAI) of**
 3 **vascular plants and *Sphagnum* is displayed. The observed C pool was calculated from mass (Xing**
 4 **et al., 2010) assuming an average C content of 40% in peat [Scanlon and Moore, 2000] and of 51%**
 5 **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		

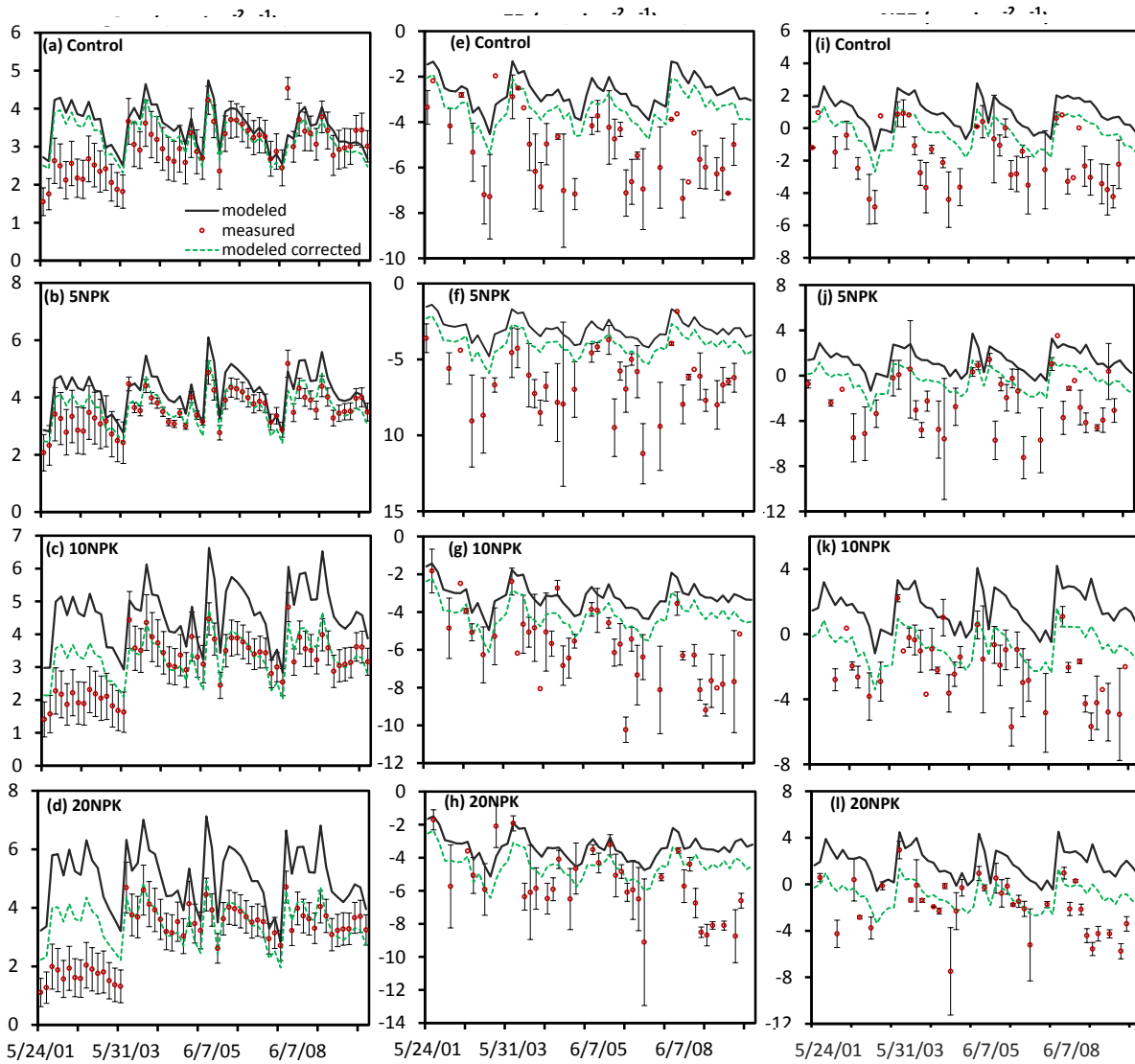
6

7 * Values were estimated from the observed *Sphagnum* biomass and a specific leaf area of 0.02 m² g⁻¹.

8

1
2
3
4
5
6
7

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, 2008. The green dotted lines represent weekly averaged CO₂ 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.

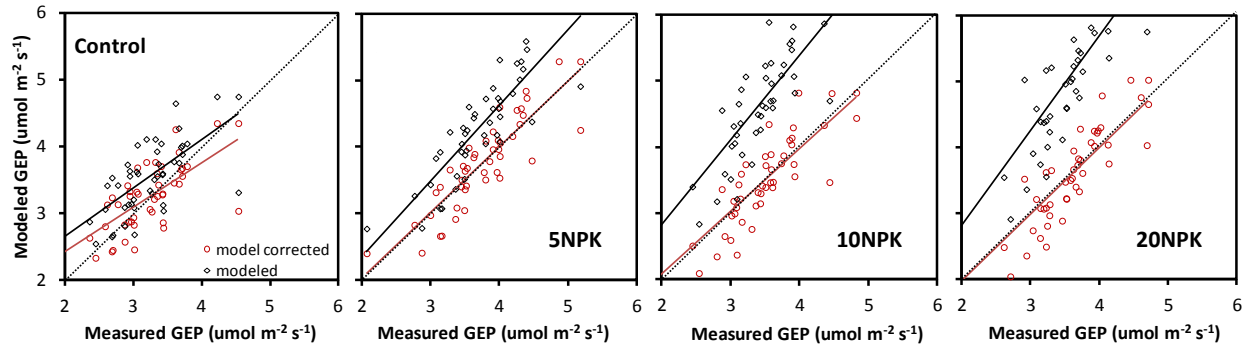


8
9

10 ** The observed GEP was reconstructed from the observed PAR (half-hourly) and the derived GEP-PAR
11 relations based on the recorded GEP at full, half, quarter light and dark conditions. The GEP-PAR
12 relations were calculated for each year and each treatment, with exceptions in 2005 and 2008 when only
13 the full light measurements were available. A GEP-PAR equation was derived from all the available data
14 between 2001 and 2008 to calculate the GEP in 2005 and 2008. The observed NEE was obtained from
15 $NEE = GEP + ER$.

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

4

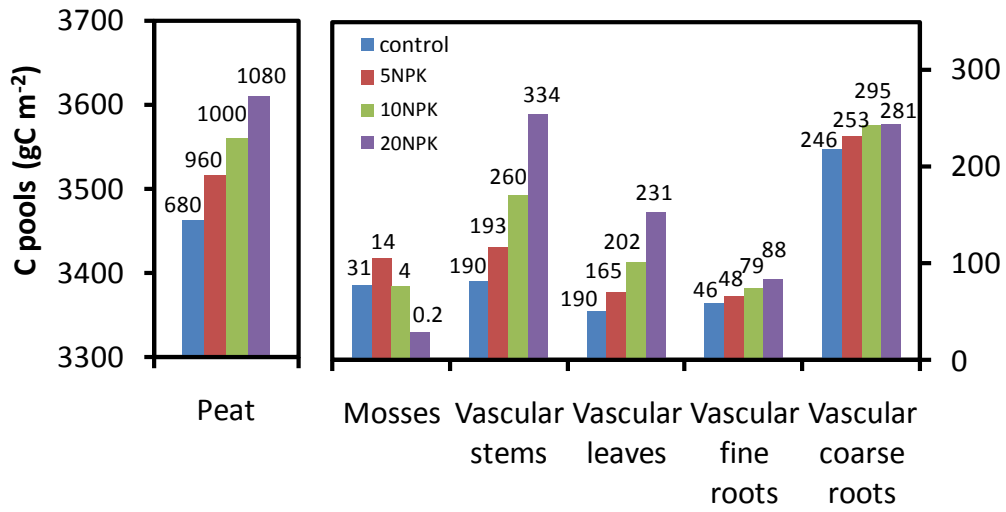


5

6

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

3

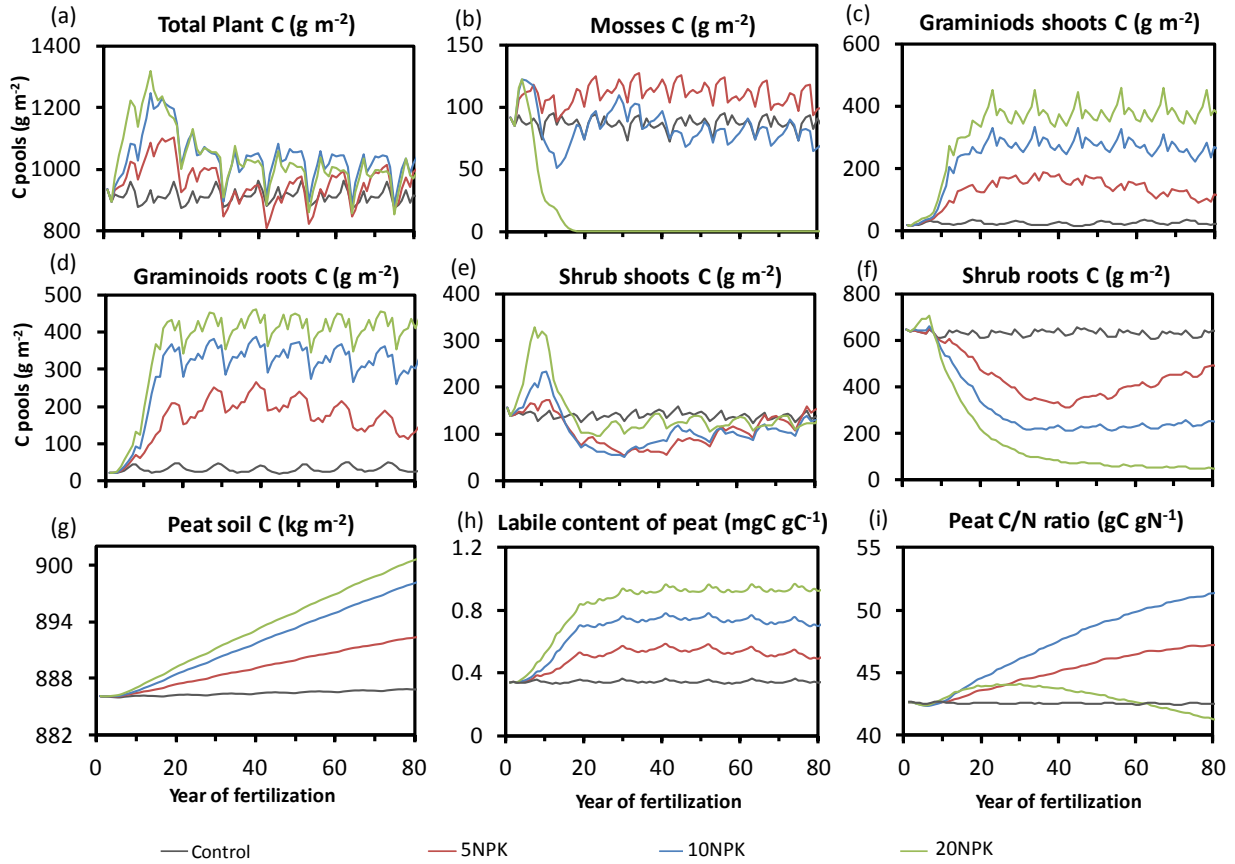


4

5

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

4



5

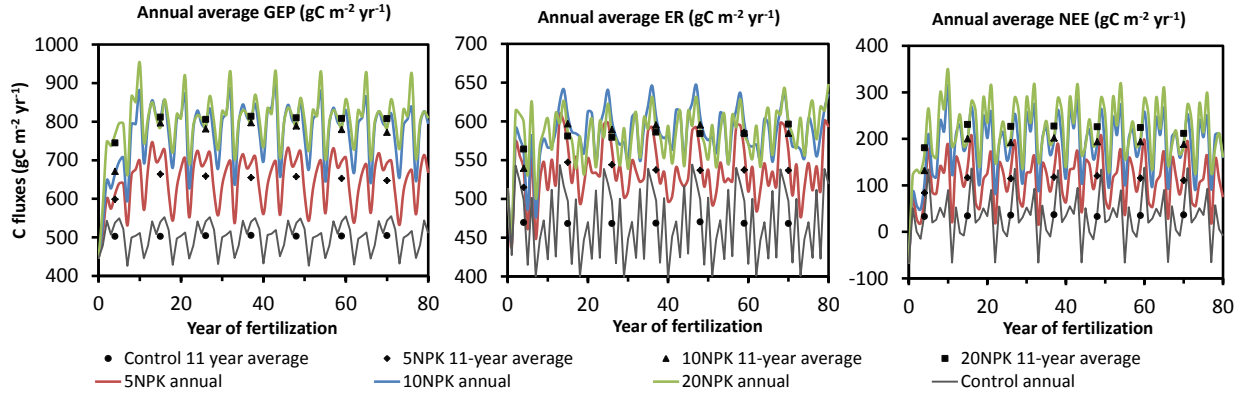
6

7

8

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

4



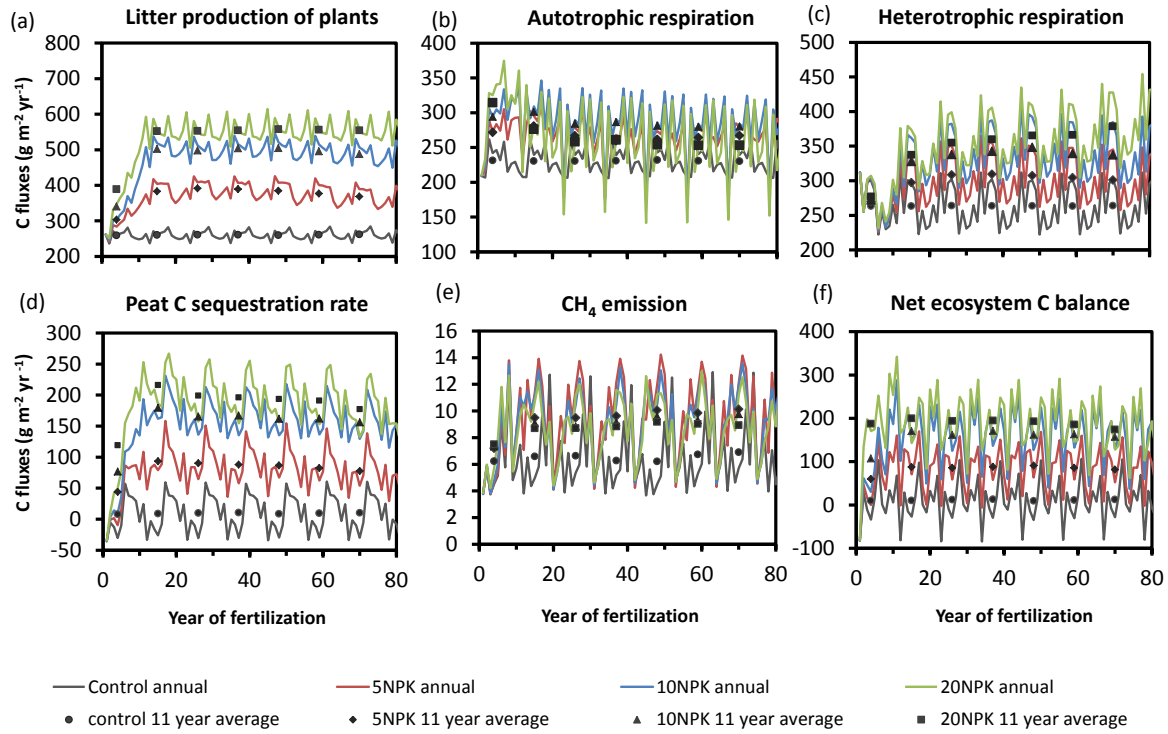
5

6

7

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

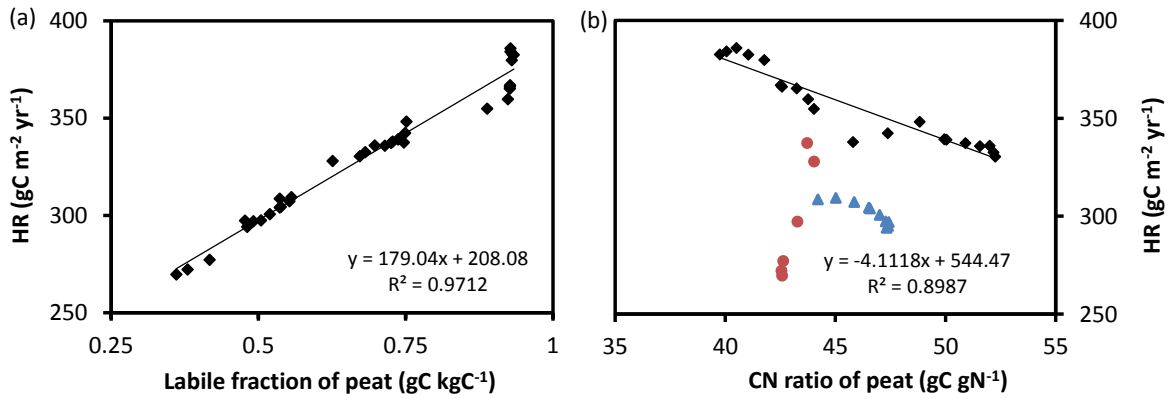
2



3
4
5

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

6

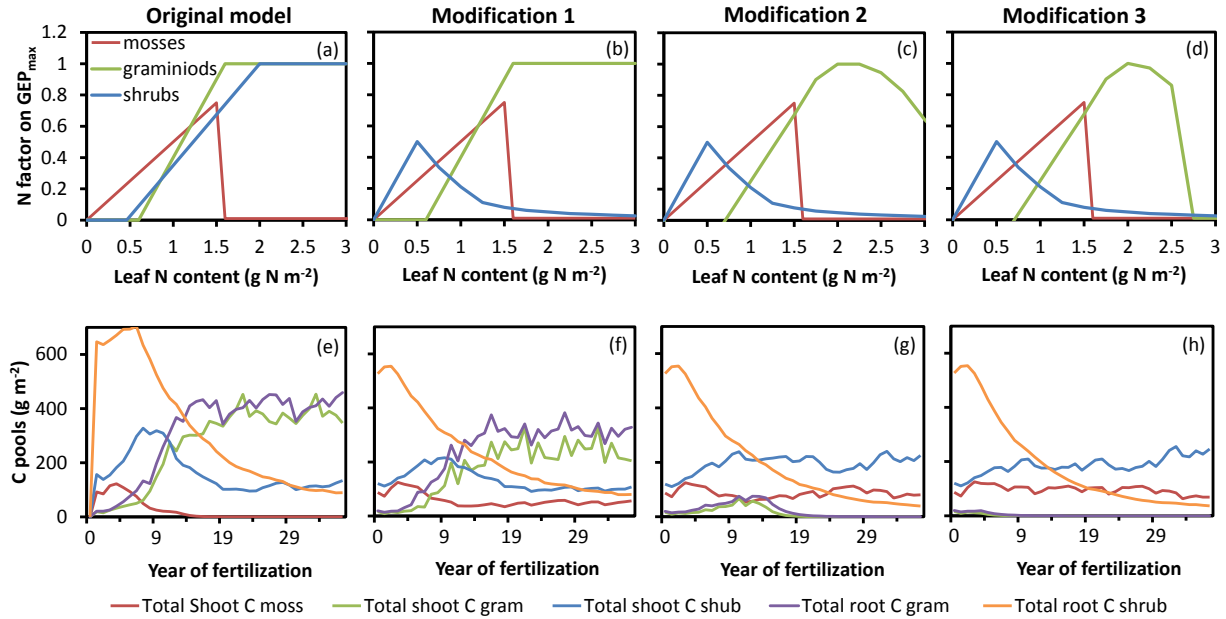


7

8

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

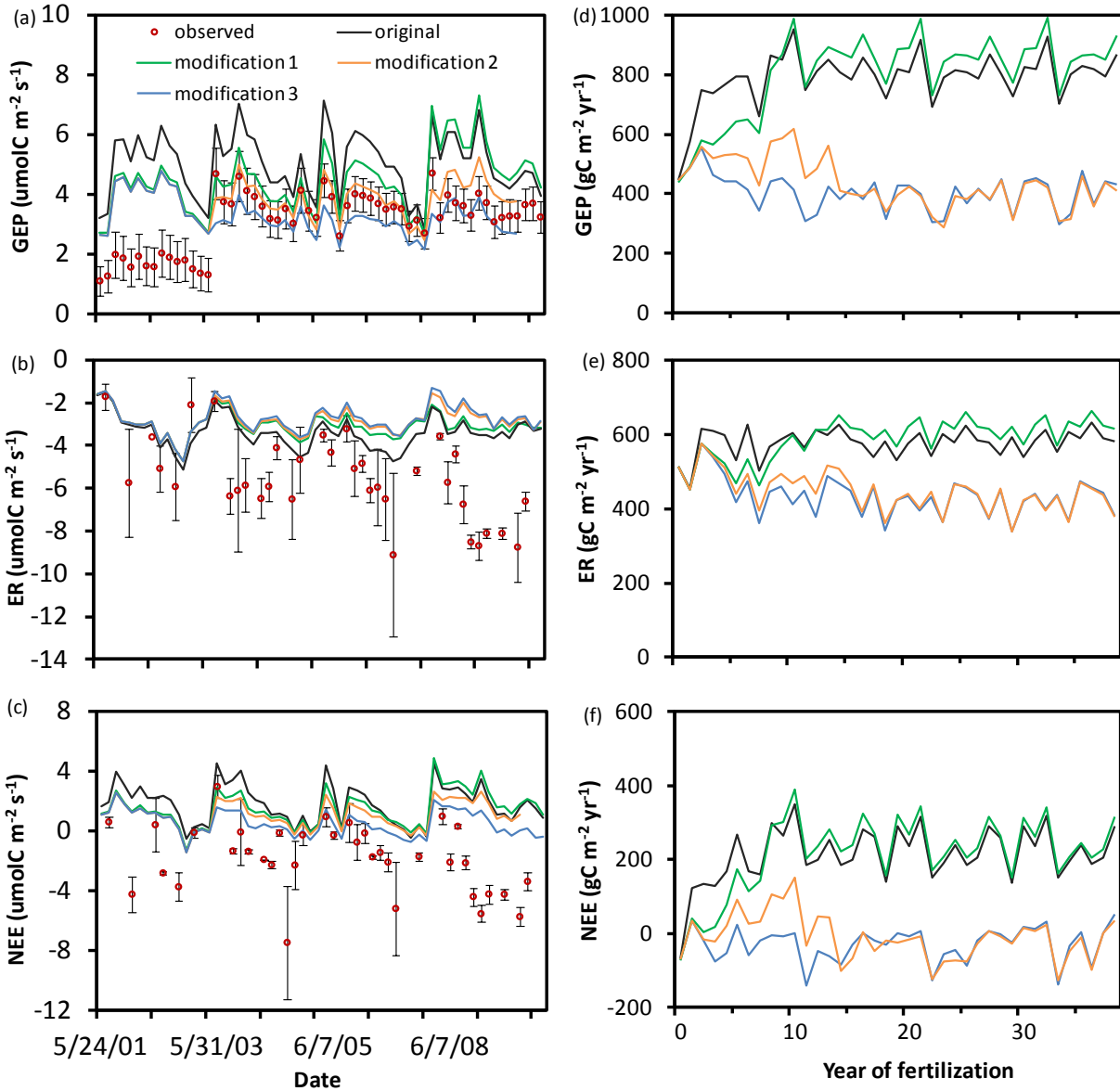
8



9
10

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

5



6

7

8

9