# Modeling alternative states of an ombrotrophic bog with experimentally deposted nitrogen

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## Abstract

Alternative states of an ombrotrophic bog subject to experimentally deposited N at 1.6, 3.2 and 6.4 gN m-2 yr-1 were analyzed using the PEATBOG model The study predicted discontinuous responses of the peatland ecosystem to differing N deposition and a lack of recovery after 15 years of fertilization with 6.4 gN m-2 yr-1, which indicated a regime shift of the modeled ecosystem. In combination drought reduced the resilience of the system and contributed to the regime shift. Internal feedbacks, such as from vegetation to the water table depth, may interact with the external drivers of nitrogen and climatic conditions and alter the responses of the bog ecosystem. The result suggested that the state of a bog subject to N deposition may be highly uncertain due to a dominant feedback loop that emerged from the all disturbances that include also climatic conditions. The finding highlighted the need for quantifying the relative importance of multiple disturbances systematically to predict the potential shift of state a peatland ecosystem to N deposition in a changing environment.

## Introduction

In nutrient poor ecosystems such as bogs, nitrogen enrichment usually favors fast-growing species over the native species (Porter et al., 2012). Expanding of dwarf shrubs and grass *Molina,* at the expenses of *Sphagnum* was reportedin European bogs due to global change including elevated N deposition (Hogg et al., 1995;Nordbakken, 2001;Gunnarsson et al., 2002). The impeded growth of *Sphagnum* (Gunnarsson and Rydin, 2000;Limpens and Berendse, 2003b) along with the stimulated growth of vascular covers (Wiedermann et al., 2007;Sheppard et al., 2011) has been verified by experimentally adding N to peatlands. *Sphagnum* mosses as the key native species in ombrotrophic bogs are highly adapted to the nutrient poor environment and are characterized by a strong N retention and efficient N use (Aerts et al., 1999). The morphological and physiological traits of *Sphagnum* support an effective uptake of deposited N for biomass growth and establish a soil environment poor in N, which assists when competing against vascular plants (Malmer et al., 1994). The moss “nitrogen filter” may fail, however, when excessive N is deposited to the peatlands, which enriches the soil and promotes the growth of vascular plants (Lamers et al., 2001;Heijmans et al., 2002). Enhanced shading (Malmer et al., 1994;Berendse et al., 2001) and water stress (Tomassen et al., 2004;Eppinga et al., 2009) along with an increase in vascular plant biomass can ultimately eliminate *Sphagnum* from the plant community and lead to subsequent changes in the C and N cycling in the peatlands.

Changes in plant cover and characteristics and related autrotrophic processes alter the ecological feedback loops that stabilize the ecosystem. *Sphagnum* mosses serve key ecological functions in maintaining the acid, cool, moist and nutrient poor environment of peatlands (Turetsky, 2003). Vegetation shifts in peatlands from moss-dominated to vascular-dominated raise, for example, the decomposability of the peat by producing litter that contains less lignin, polyphenol and acid-unhydrolyzable residue (Aerts et al., 2006;Limpens and Berendse, 2003a;Breeuwer et al., 2008;Bragazza et al., 2006;Bragazza and Freeman, 2007). Additional carbon loss was reported due to accelerated decomposition of fresh peat in fertilized bogs as well, accompanied with decreases in the growth (Gerdol et al., 2007;Bragazza et al., 2012). Accumulation of dissolved N in the soil water (Xing et al., 2010;Sheppard et al., 2013) and leakage of N2O (Lund et al., 2009a) were furthermore recorded in N fertilization experiments in European and Canadian bogs.

Moreover, a shift from C and N uptake to release along with vegetation change may enhance global warming (Gorham, 1991;Limpens et al., 2008), which in turn may lead to additional export of C and N from peatlands though the biogeochemical cycles (Moore et al., 1998;Freeman et al., 2004). The dominant feedback loops of the peatland that maintains the vegetation and functioning may be diverged in such cases, which can lead to shifts of the ecosystem to alternative and persistent states (Turetsky et al., 2012), defining as “regime shifts” (Turner et al., 1997). Resilience is defined as the “persistence of relationships within a system” and it measures the “ability of these systems to absorb changes of state variables, driving variables and parameters and still persist” (Holling, 1973). Reduction of resilience decreases the size of the basin of attraction and the amount of perturbations for bringing the ecosystem to an alternative steady state, which raises the risks of regime shifts for an ecosystem (Scheffer et al., 2001).

In this study, regime shifts of the peatland ecosystem due to N deposition were studied using the process based C-N model PEATBOG that has been parameterized and validated for the Mer Bleue Bog in previous studies (Chapter 2 – 4). The model is capable of tracking C and N throughout the vegetation and soils and of identifying the biogeochemical feedbacks in the short-term and long-term. In the previous studies (Chapter 3 – 4), the model was applied to study the effects of N on the C and N cycle in the Mer Bleue peatland using a long term N fertilization experiment. This study examined alternative steady states that the peatland approached with N deposition and the effect of a second, concomitant disturbance. In particular, the simulations were designed to explore how the interacting feedback loops are altered by N deposition and how the alternative states of the peatland are established.

## Material and methods

### Empirical data base

The N fertilization experiment was conducted on the Mer Bleue Bog (45.51N; 75.48W) located 10km east of Ottawa, Ontario. The Mer Bleue Bog is a raised acidic ombrotrophic bog of 28 km2 with peat depth ranging from 5 to 6 m at the centre to <0.3 m at the margin (Roulet et al., 2007). The vegetation coverage is dominated by mosses (e.g. *Sphagnum capillifolium, S. angustifolium, S. magellanicum and Polytrichum strictum*) and evergreen shrubs (e.g. *Ledum groenlandicum, Chamaedaphne calyculata).* Some deciduous shrubs *(Vaccinium myrtilloides*), sedges (*Eriphorum Vaginatum),* black spruce *(Picea marinana)* and larch also appear in some areas (Moore et al., 2002). The annual mean air temperature is 5.8 degrees and the mean precipitation is 910 mm (1961-1990 average; Environmental Canada). The coldest month is January (-10.8 ºC) and the warmest month is July (20.8 ºC) (Lafleur, 2003). Background N deposition was estimated at the high end in Canada at ca. 1.5g m-2 yr-1. Wet inorganic N deposition amounted to about 0.8 g m-2 yr-1 and NO3- contributed 60% to this number (Moore et al., 2005a). Nitrogen was deposited as irrigate 7 times in the growing season as NH4NO3 and PK as KH2PO4 approximately every 3 weeks to triplicate plots from May to August from 2000 and 2001, respectively (Bubier et al., 2007). This load was equivalent to an annual deposition of 1.6, 3.2 and 6.4 gN m-2 s-1. A 15N tracer was applied as NH415NO3 (10% 15N) by substituting the last fertilization dose in 2007 (Xing et al., 2010). Vegetation samples were collected twice at the beginning of 2000 and 2008 during the growing season and peat cores and soil water were sampled 3 times from July to October in 2007 (Xing et al., 2010).

### Model input, strategy and evaluation

The PEATBOG model is implemented in stella® and calculates daily C and N pools in leaves, stems, fine roots and coarse roots in three plant functional types (PFTs), and in labile and recalcitrant soil organic matter pools and in the dissolved phase in soil water (Wu and Blodau, 2013b). It consistently emphasizes mass balance principles and the dynamic interplay of production, consumption and translocation of materials throughout the ecosystem. The required model inputs include geographic location and local slope of the site, daily precipitation and photosynthetic active radiation (PAR), daily snow depth record, annual average and range of air temperature, atmospheric CO2, CH4 and O2 levels, annual N load and PFT biomass. The daily average precipitation, PAR, air temperature and snow depth from 1999 to 2009 were derived from continuous measurements from *fluxnet Canada* ([http://fluxnet.ccrp.ec.gc.ca](http://fluxnet.ccrp.ec.gc.ca/)) every 30 minutes. Gaps were filled by linear interpolation (less than 2 hours) and otherwise by repeating the corresponding period of time from the closest available dates. The spin-up of the model was conducted to steady state for more than 10000 years at a daily time step with repeated time series of all input.

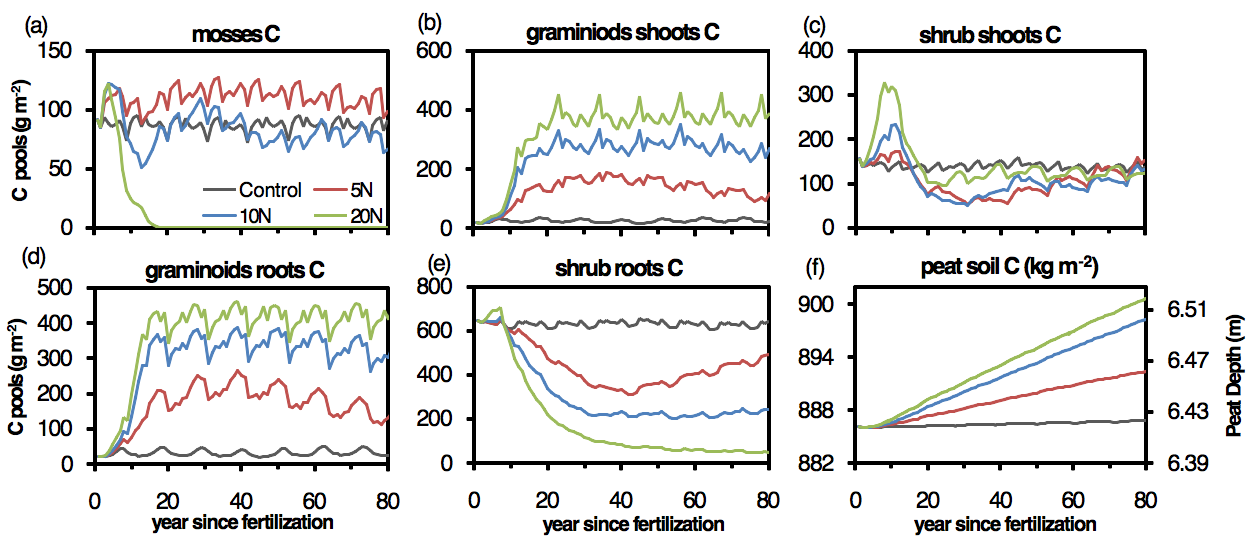
In the previous studies (Chapter 3 – 4), the model satisfactorily simulated the observed impact of experimentally added N on the vegetation and C and N cycle in the N(PK) fertilization experiments in the Mer Bleue Bog. Model N input was from atmospheric N deposition at 1.5 gN m-2 yr-1 and N fertilizers. N deposition was composed of NH4+ (30%), NO3- (43%) and DON (27%) (Moore et al., 2005a). Fertilization with N in model and field were identical at levels of 1.6, 3.2 and 6.4 gN m-2 yr-1, equally supplied as NH4+ and NO3-. Fertilizer was applied on one day in intervals of 21 days from mid-May to late August. Simulations were conducted with no constraints posed by P or K availability and were comparable to the NPK treatments in the field.

The study comprised two steps. In the first step, the alternative states of the simulated peatland were assessed for their stability based on the guidelines reviewed and categorized in (Schröder et al., 2005): (1) discontinuity in the response to an environmental driving parameter, (2) lack of recovery potential after a perturbation, (3) divergence due to different initial conditions and (4) random divergence. The first two criteria on the discontinuity of responses and the recovery potential from the nitrogen perturbation were adopted as the criteria in this study, as latter two criteria require a differing initialization of the model and were not affordable at this time. The discontinuity was assessed by examining the state variables of the pools in time series at varying annual N deposition levels. The recovery potential was tested by ceasing experimental nitrogen fertilization after 15 years, as is planned (Moore, pers. Communication). In the second step, we ran two scenarios to study the impact of an additional disturbance on the steady state and model resilience. In the first scenario we raised the water table depth according to observations of the fertilized plots (Juutinen et al., 2010). In the second scenario, the competition between graminoids and shrubs was manipulated by modifying the canopy structure implemented in the model.

## Results and Discussion

### Responses of the Mer Bleue Bog to nitrogen

Overall, nitrogen deposition caused strong and rapid changes in the model’s state variables, such as the C and N pools in the plants and in the peat, during the first 20 years. This period was followed by slower and more moderate changes in those state variables (Fig. 5.1). The changes increased furthermore disproportionately with increasing N deposition (Fig. 5.1). The trends of the state variables were discontinuous in time and with N load. The carbon pool in mosses sustained higher levels in the 5N and 10N simulations than in the control simulation after 20 years. In the 20N treatment, however, this C pool continuously declined to disappearance at the 15th fertilization year (C pool in mosses < 1g m-2 in the model). N pools in plants were significantly altered with the highest N deposition in absence of mosses. N pools in the graminoids, which dominated the peatland at the end of the simulation in the 20N treatment, were approximately 3 times larger than that in the control (Fig. 5.1h, 5.1j). Nitrogen in mosses increased more rapidly in the 10N than in the 5N simulations during the first 10 years. After that however, both treatments returned to a similar N pool in mosses, despite their differing C pool. The responses of C and N pools in the three PFT showed similar hysteresis patterns. The accumulation of C and N in shrubs substituted for declining accumulation in mosses until the 10th fertilization year, when graminoids began to rapidly accumulate the elements and replaced the other groups as major sink (Fig. 5.1). Peat acted as larger C and N sink when N deposition was raised yet in a non-linear fashion. The C pool in peat similarly increased in all treatments (Fig. 5.1f). With regard to the peat N pool, more N was sequestered in the 20N compared to the other treatments (Fig. 5.1l). Overall the retention of C and N in the peat decoupled and more N was retained, which was also reflected in the falling C/N ratio towards a new steady state of the system (Fig. 5.1o).



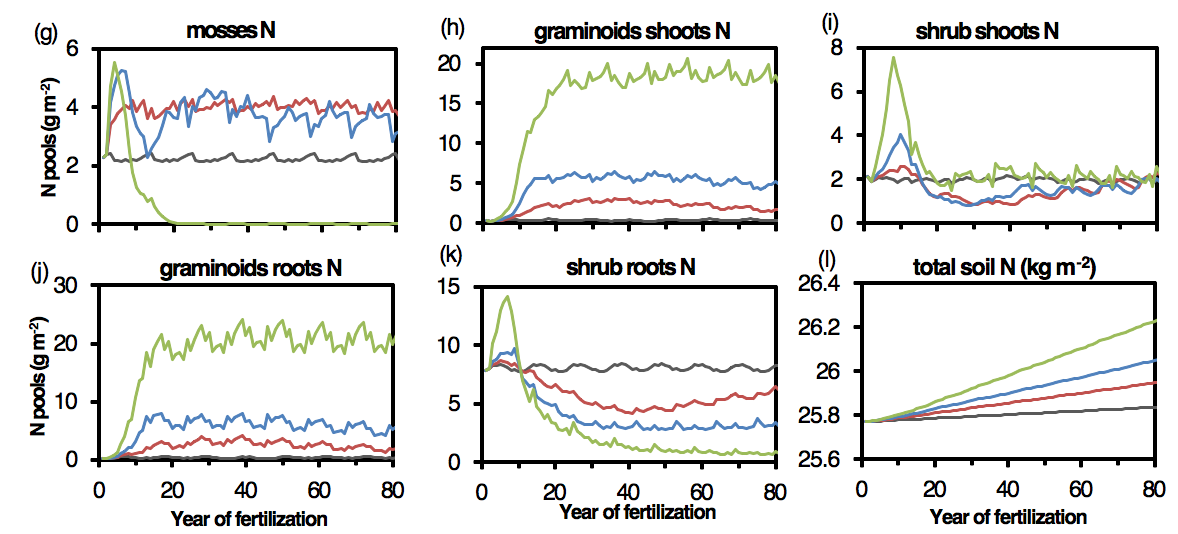


Figure 5.1 Simulated annual average C pools (a to f and l, unit: gC m-2) and N pools (g to l and n, unit: gN m-2) in the plants and C/N ratio in the upper 40cm of peat (o) over 80 years of fertilization.

The results were generally in line with predictions from the conceptually oriented system dynamics model for peatlands (Pastor et al., 2002). They illustrate the shift from moss monoculture to moss-vascular coexistence steady state with an increase in nutrient input to peatlands (Pastor et al., 2002). The simulated plant composition changed with fertilization levels and in the 20N treatment a PFT was finally lost (Fig. 5.2). The level of fertilization distinctly mattered for the dynamics and steady state of the simulated vegetation. In the simulated 5N treatment, plant composition remained similar as in the control. In the 10N treatment, however, the carbon pool in graminoids was raised at the expense of shrubs. Shrubs partly recovered in the simulated 10N and 5N treatment, whereas they did not in the simulated 20N plots (Fig. 5.2a, 5.2c). Somewhat unexpectedly, given the severe N load of 3.2 g m-2 yr-1, mosses continued filtering N in the 10N treatment and kept dissolved N concentrations low (Fig. 5.3). This was not the case at all in the 20N simulation, however, where mosses were extinct after 15 years. In the model the N in the vascular plants strongly increased (Fig. 5.1h, 5.1j)following the accumulation of N in the soil water in the upper zone (Fig. 5.3). The increases in the vascular roots, however, led to lower N concentrations in the soil water in the deep rooting zone (Fig. 5.3). The level of nitrogen deposition thus strongly mattered for the state of the simulated bog ecosystem: At loads of 6.4 gN m-2 yr-1 a new kind of peatland ecosystem evolved, whereas at lower levels the original state was only modified. It can be speculated that under the chosen temporal fertilization regime, which in itself matters (Chapter 4), a nitrogen deposition threshold, or critical load, is found somewhere between 3 and 6 gN m-2 yr-1.

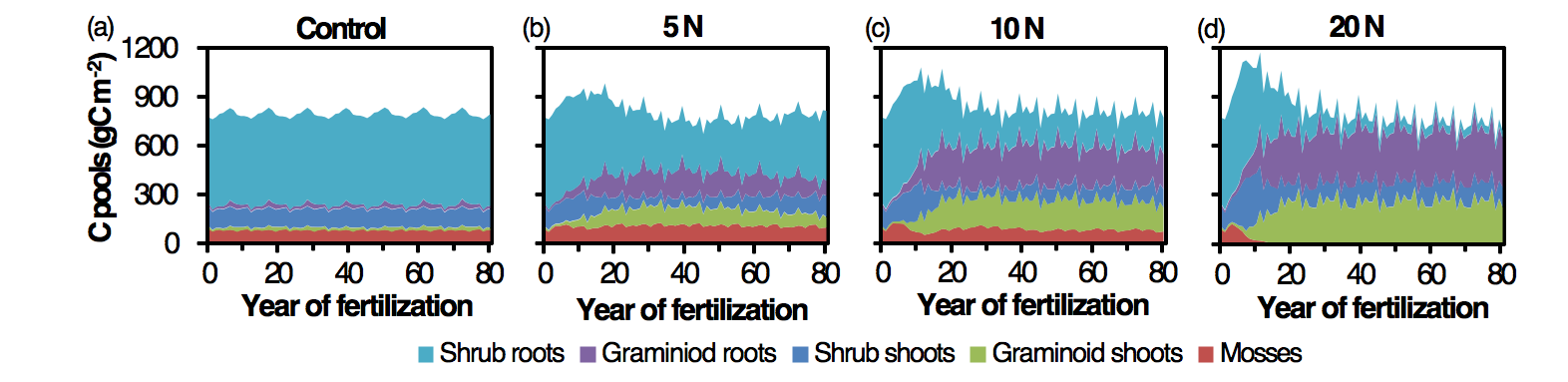


Figure 5.2 Carbon pools in the shoots and roots of plant functional types during 80 years of fertilization.

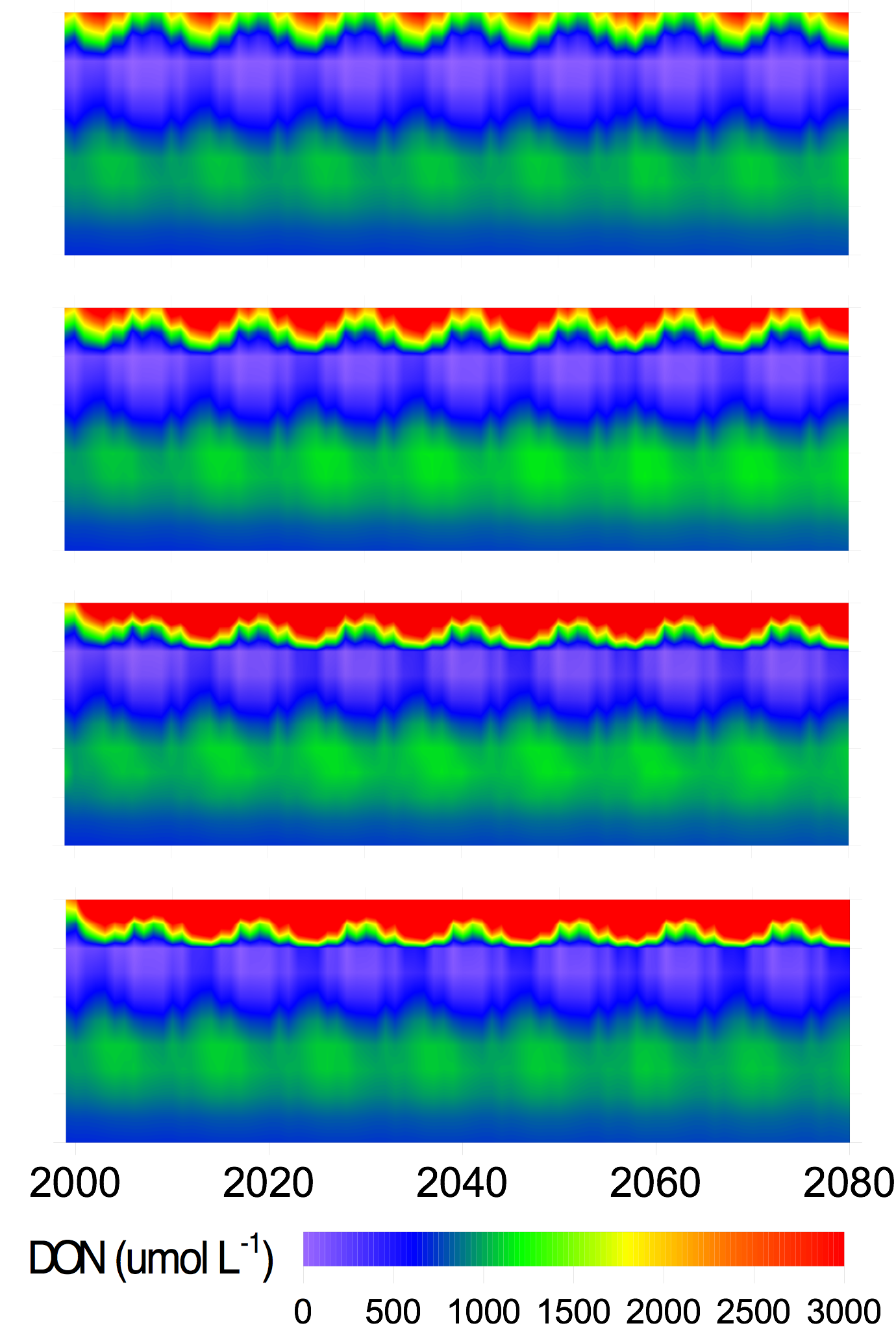
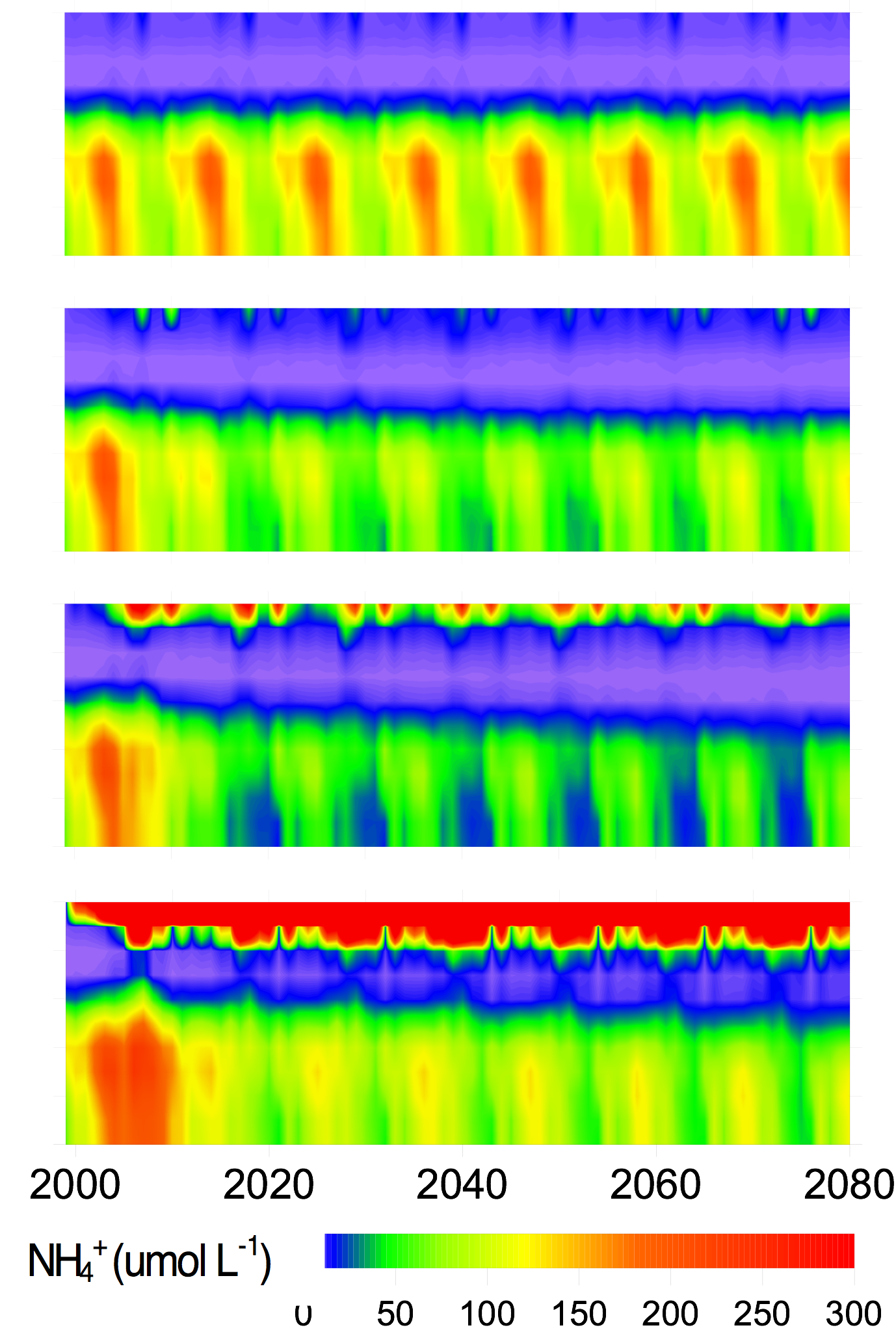
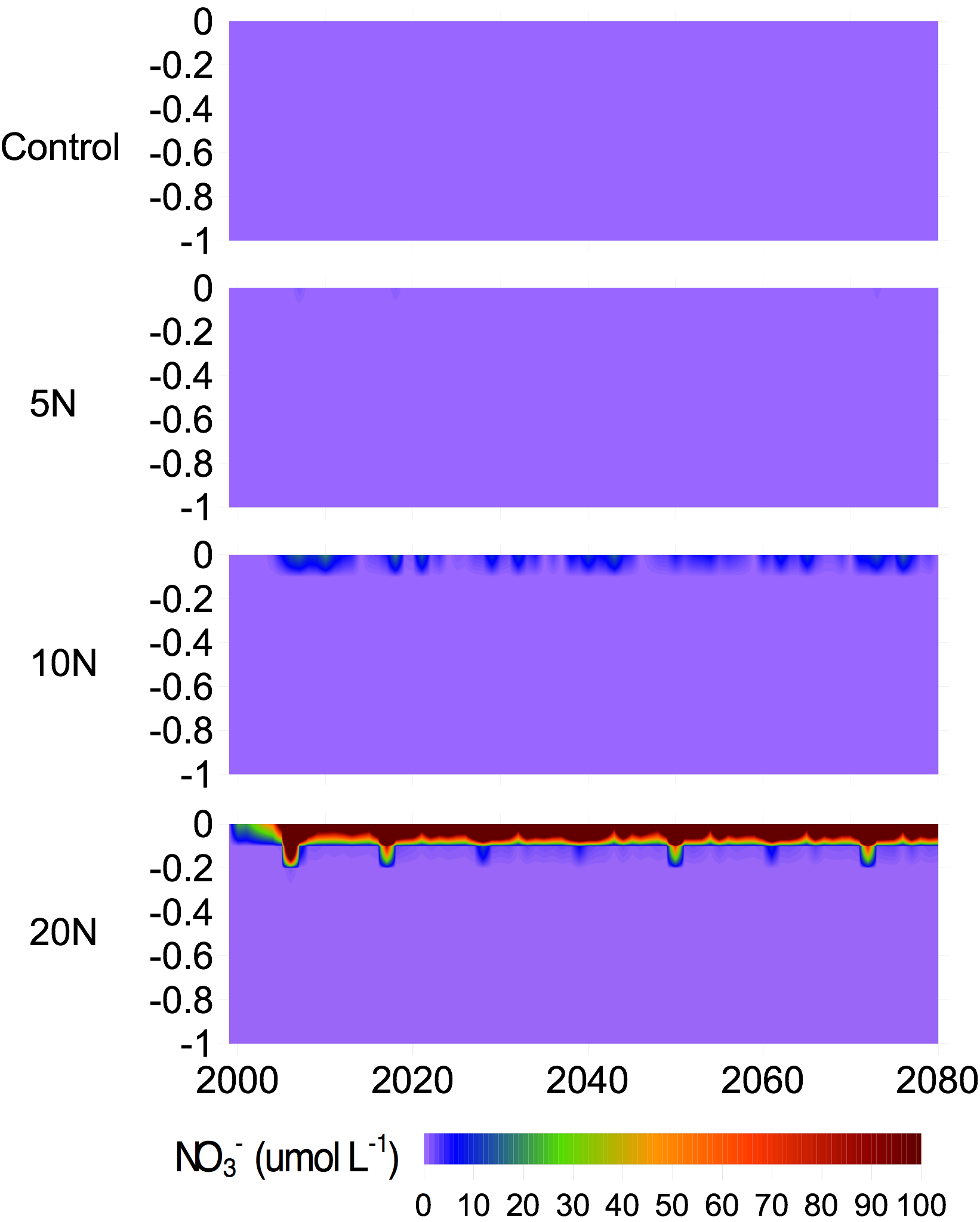
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Figure 5.3 Simulated concentration profiles of NH4+, NO3- and DON (unit: umol L-1) in the soil water over 80 years of fertilization.

### Recovery potential after experimental nitrogen deposition

The reversibility of changes in the state of the simulated bog after the 14-year fertilization had ceased demonstrated the existence of alternative steady states under elevated N load and the resilience of the system to N deposition at moderate N loads. Within 25 years after the nitrogen fertilization was ceased, the vegetation nearly returned to the initial state in the simulated 5N and 10N treatments (Fig. 5.5a). In the 20N simulation however, the bog remained shrub-dominated in absence of mosses (Fig. 5.5b). The model therefore suggested that different ‘basins of attraction’ exist after the 14-year perturbation. The reversibility of the changes at low levels of N fertilization suggests that mosses are critical for the resilience of ombrotrophic bogs. Similar to our findings, mosses were found important for the robustness of C sequestration using the Holocene Peat Model (HPM) in climate change scenarios (Turetsky et al., 2012). In their study, mosses appeared critical in maintaining cool conditions in the soil and in buffering water table variation with precipitation. Our model rather emphasized the N filtration function of mosses for lowering dissolved N concentration in the soil. The negative feedback from mosses on the vascular plants may be restored in the post-fertilization period, resulting in the recovery trend of the changes in vegetation. After N fertilization had ended in the 5N and 10N simulation, mosses were able to immobilize the deposited background N. Thus, in these treatments the deposited N entered the soil as recalcitrant moss litter, which limited N mineralization and N availability for the vascular plants. The impact of moss litter quality on mineralization was illustrated by the response of C/N ratios to N deposition (Fig. 5.1) and the resulting changes in heterotrophic respiration rate, as discussed in Chapter 3 (Fig. 3.6).

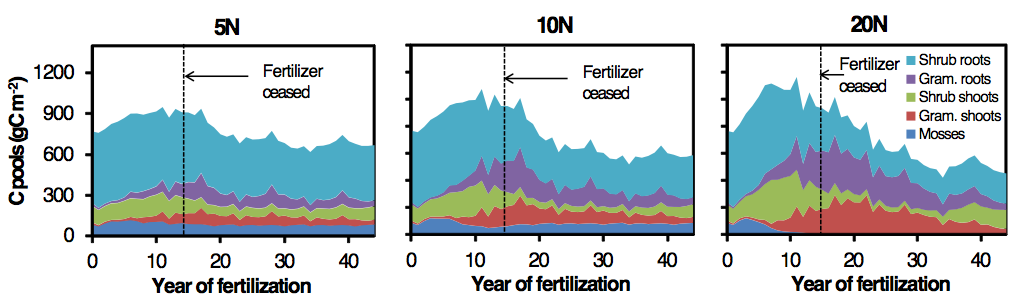


Figure 5.4 Simulated C pools (unit: gC m-2) in the mosses and the shoots and roots of graminoids and shrubs in the fertilized plots with cessation of N fertilization in the 15th years.

### Interacting feedback loops control the alternative states of the system

#### Nitrogen deposition and change in water table depth

The model showed that regime shift occurred following severe disturbances from both N deposition and desiccation in the 20N treatment. In Chapter 4, a toxic effect was identified as main cause for the negative impact of N deposition in this treatment. The effect resulted from a high N concentration exceeding the uptake capacity of mosses. Meanwhile, in the dry years during the first 10 years of the simulations mosses desiccated. The simulated water table depth declined down to 0.8 meters below the peat surface in 2010 (Fig. 5.6). The combination of both stressors caused the breakdown of mosses followed by the invasion in vascular plants in the simulated 20N treatment. In other words, the ecosystem was pushed beyond a threshold towards an alternative steady state by the two concurrent disturbances. The simulation results are in line with empirical findings from the site, where mosses were early lost in the fifth year in the 20N plots compared to other fertilized plots in European bogs (Juutinen et al., 2010). The fast response was attributed to the high background deposition level of N and the low water table depth of the site (Juutinen et al., 2010). In particular, the low water table ranging from -55 to -41 meter during 2001 and 2007 may have contributed to the decline of mosses observed since 2003 (Juutinen et al., 2010), similar to the model results in the 20N treatments. Moreover, mosses did recover in the 5N plots from the wet year 2008 on in the field (Juutinen et al., 2010), resembling the simulated recovery in the 10N treatment since the wet year in 2011 (Fig. 5.1).

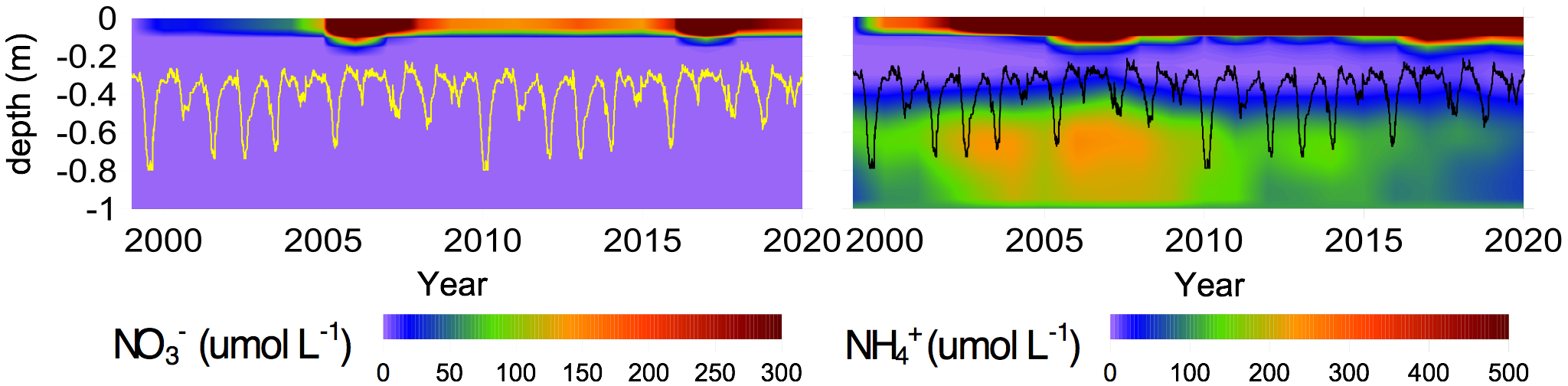


Figure 5.5 Simulated annual average concentrations of NH4+, NO3- (unit: umol L-1) in the soil water over 20 years of fertilization at 6.4 gN m-2 yr-1 from 2020 to 2020. Yellow and Black lines indicate daily water table depth (unit: m).

Bog ecosystems are able to adjust the water table depth through internal feedbacks, for example by changing physical properties of the peat. The summer water table depth in the 20N plots was recorded 14cm higher than in the control in 2008 (Juutinen et al., 2010). The significant raise of the water table depth occurred after 5 years of the *Sphagnum* loss from the plots. An increase of the water table depth was also reported accompanying loss of *Sphagnum* in a boreal fen that had been fertilized with 3 gN m-2 yr-1 for 13 years (Eriksson et al., 2010). The water table raises may be explained by feedbacks from the altered vegetation (Larmola et al., 2013). The physical properties of the shallow peat at the Mer Bleue Bog, for example, were changed by changing litter input from the vegetation (Wendel et al., 2011). The dominated shrubs accelerated the turnover rate of leaves and sustained more abundant aboveground biomass as well as a higher litter production in the 20N plots than in the others (Juutinen et al., 2010). The litter accumulation was 410g m-2 in 2005 and approximately 300 g m-2 in 2008 in the 20N plots, which was 10 and 6 fold the litter accumulation in the control plots. The litter of shrubs decompose faster than *Sphagnum* (Moore et al., 2007) and, therefore, formed more compacted peat with a higher bulk density in the 20N plots (Bubier et al., 2007). On the other hand, the expanded vascular plants may have raised the transpiration, and led to lower soil moisture in the surface peat in the fertilized plots compared to the control plots (Wendel et al., 2011), despite a higher water table depth.

In the model, we implemented the observed changes in the water table depth and examined the potential impact on the state of the system by examining internal feedbacks from vegetation to water table depth. The increase of water table was implemented in the model simply by a step-raise of 14 cm at the beginning of the 9th fertilization year, assuming the raise was sustained in the rest of the years. The simulation results showed immediate flourishing of mosses after the water table rise. The moss C pool recovered from 35gC m-2 in 2008 to 68 gC m-2 within 5 years remained similar thereafter (Fig. 5.7a). The bog shifted to be graminoid-moss dominated with rarely any shrub remaining. Compared to the original simulation, graminoids were now more competitive than shrubs in this scenario. The dominance of graminoids was not surprising given the greater tolerance of the simulated graminoids to wet conditions. Comparing the outcome to the previous simulation, we identified the coincidence of drought and toxic N levels as a key for the vegetation shift. The comparison of the simulation further suggests that mosses may be more tolerant to N deposition in wet environment. In support of this argument, negative effects of N on *Sphagnum* moss were found exacerbated when climatic stresses were introduced and mitigated when they were removed (Carfrae et al., 2007). On the physiological level, moisture was found to restrain the photosynthetic capacity of *Sphagnum* at high N deposition (Granath et al., 2009). The mechanism behind this phenomenon may be the increase of chlorophyll content under low light conditions, which compromises the protection against photo-oxidation in mosses (Bonnett et al., 2009). Tomassen et al. (2004) argued that desiccation may have played a more important role than N deposition in triggering the expansion of *Molinia* and *Betula* in the Dutch bogs. Their findings agreed with a lack of change in vegetation over 14 and 17 years in two bogs receiving high and increasing atmospheric N depositions, suggesting robustness against in N deposition when water regime remained unchanged (Hájková et al., 2011).

#### Nitrogen deposition and plant competition for light

The growth and photosynthesis of mosses was found to be inhibited by the low light level at the moss layer in the fertilized plots of the Mer Bleue Bog (Chong et al., 2012). Enhanced shading by vascular plants may have reinforced the negative feedbacks of N on mosses and may have accelerated the extinction of mosses in the 20N treatment. While we have no means to examine such effects by internally driven modifications of the canopy structure we used changes in the model structure to gain some insight into this issue. In the ensuing simulations, the canopy structure of the PFTs in the model was modified to differently represent light competition among PFTs. In the original model, PFTs were assumed to colonize their own canopy layer each and a sequence of canopy layers was stipulated in that mosses were shaded by shrubs and graminoids, and shrubs by graminoids only (Wu and Blodau, 2013b). Accordingly the competitive advantage of graminoids over shrubs and mosses was overestimated, as no shading was allowed from other PFTs on graminoids. In the modified structure, shrubs and graminoids co-occupied the uppermost canopy layer. The share of the canopy depended on the share of the leaf area of the PFT. The modified model simulated a colonization of shrubs in the peatland after 10 years of fertilization with 6.4gN m-2 yr-1 in the 20N plots (Fig. 5.7b). The results from the modified model showed less discrepancy to empirical observations than the original model, regarding the vegetation dynamics during the first 12 years of the experiments (Xing et al., 2010). The quick elimination of mosses in the modified scenario was attributed to the more rapid increases in the shoots of vascular plants (Fig. 5.6c).

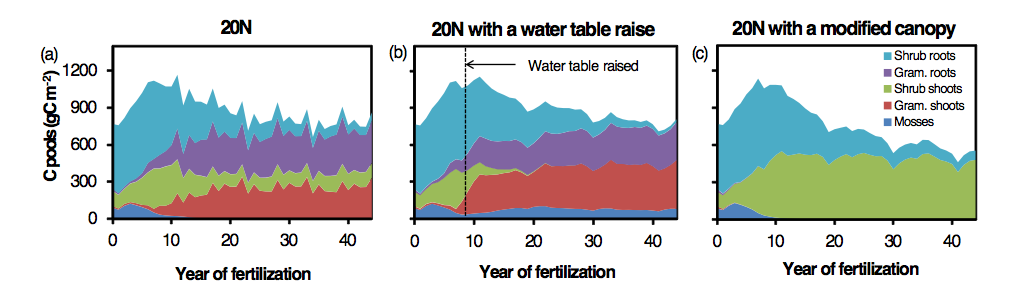


Figure 5.6 Simulated C pools in mosses, graminoids and shrubs shoots and roots in the 20N treatment in the original model (a) and in the modified model with (b) a raise of water table by 14cm after 8 years of fertilization, and (c) a canopy structure with graminoids and shrubs shoots on the same canopy layer.

This modification maximized the competition for light among shrubs and graminoids, assuming that shrubs do not overgrow graminoids (Heijmans et al., 2008). Considering the original model structure minimized the light competition of shrubs with graminoids, this scenario and the original scenario represented the two extremes of light competition between shrubs and graminoids. The results from these two extreme assumptions characterized a shrub and graminoids dominated system respectively, implying a large range of possibilities of the plant composition in the fertilized 20N plots in the long-term. The realism of these possibilities is not yet fully clear. In the Mer Bleue Bog, shrubs were suggested incapable of raising the photosynthetic capacity and to be less competitive than other PFTs in the long-term, despite the great increase of the shrub biomass in the fertilized plots within the experimental period (Bubier et al., 2011b;Larmola et al., 2013). Indeed, *Eriophorum* inhibited further increases of *Erica* biomass after 5 years of dry N fertilization in a Scottish Bog (Sheppard et al., 2011). Previously, graminoids were reported to compete more successfully than shrubs and other evergreens in boreal tundra with experimentally manipulated N deposition (Bowman et al., 1995;Chapin and Shaver, 1996;Sheppard et al., 2011). The mechanism was likely the differing utilization of the absorbed N within the plants: graminoids are able to invest the additional N on growth (Wiedermann et al., 2007), while shrubs reserve extra N as amino acids (Bubier et al., 2011b). In contrast, Kool and Heijmans (2009) argued that dwarf shrubs adapted faster to N and could successfully compete with graminoids at high N supply in peat bogs, based on a greenhouse experiment.

The modeling results suggested that the colonized canopy structure might not be sufficient for modeling vegetation competition under elevated N deposition. Canopy structures with a higher organizational complexity may need to be implemented in peatland vegetation models to improve the quality of vegetation responses to N deposition. In this study, the modified canopy structure considered the competition among vascular plants by simulating the feedback from biomass growth of plants to light inception. The growth of graminoids and shrubs was presented with this canopy structure in a simple way. Potential adaptations of the PFTs to N deposition through morphological and physiological changes may enhance the feedback through PFT growth. For example, shrubs increased the canopy height and accelerated the turnover in the fertilized plots in the Mer Bleue Bog, exerting stress on the ground vegetation through shading and litter burial (Juutinen et al., 2010). In a climate manipulation experiment, *Sphagnum fuscum* was found to be promoted in the competition with vascular plants by increasing length, which helped sustaining the plant community (Keuper et al., 2011).

#### Feedback loops that control the alternative steady states

The results showed a more limited resilience of the bog ecosystem when two disturbances, N deposition and desiccation, occurred simultaneously. Perturbing an ecosystem with a second disturbance while it is undergoing the first disturbance can alter the community state in an ecosystem (Paine et al., 1998). Rietkerk et al. (2004b) developed a dynamic model and simulated the reinforcement of the shading effects from vascular plants on mosses in a nitrogen deposition bog. In their analysis nitrogen deposition was regarded as a second perturbation to the system. They argued that nitrogen deposition reduced the basin of attraction of the *Sphagnum*-dominated system and accelerated the shift of the peatlands to a vascular-dominated state. The argument may be inherited to our study, suggesting that both drought and nitrogen deposition can reduce the basin of attraction of the *Sphagnum*-dominated system.

The result further suggested a large range of possibilities of the plant composition and the alternative state of the system with N deposition, especially in the context of climate change. The interactions among the multiple disturbances can alter the dominant feedback loop and the subsequent state of the bog system. The alternative state of the bog beyond the “valley” of the *Sphagnum*-dominated state may differ depending on the dominant loop that is merged. A conceptual diagram illustrated the interacting effects of N deposition and climatic conditions on the vegetation competition in a bog ecosystem (Fig. 5.8). Dry summers as expected from climate change predictions tend to decline the water table depth, which in turn can hamper mosses directly or indirectly through promoting the growth of shrubs and enhancing shading. Changes in vegetation however, can influence water table depth by altering physical properties of peat. Such changes were observed in the bulk density of peat in the 20N treatment in this study (Juutinen et al., 2011), and counter the lowering of water table depth by the climate. In addition to the external drivers, competition between shrubs and graminoids may change with the adaptation of plants morphologically or physiologically to the N deposition and water table depth. Finally, the dominant feedback loop is regulated by the sensitivity of the PFTs to nitrogen deposition, water table depth and shading and the relative changes of those factors. As local climatic conditions vary and responses of site-specific species to each driver differ (Bertness and Ewanchuk, 2002) across peatlands, the response of a peatland ecosystem to nitrogen deposition can be very different, as has been observed empirically.

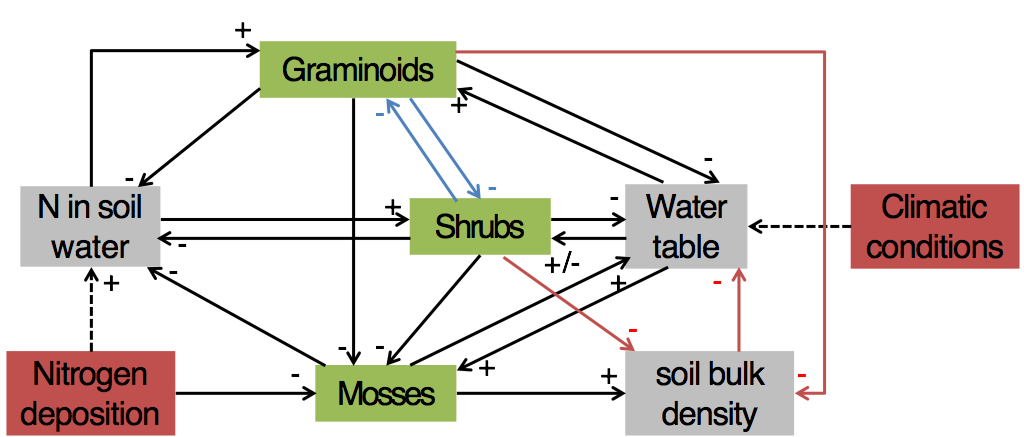


Figure 5.7 A conceptual diagram on the feedback loops showing the effects of nitrogen deposition on peatland vegetation. The red arrays indicated the feedback loops from the vegetation to water table depth. The blue arrays indicated the feedbacks that were enhanced with a modification in the canopy structure.

## Conclusion

The modeling study predicted a regime shift of an ombrotrophic bog from a shrub-moss dominated state to a graminoid-dominated state after 15 years of N fertilization with 6.4 gN m-2 yr-1. As a second disturbance that occurred concurrently with N deposition, drought was identified to have contributed to the regime shift through reducing the resilience of the bog ecosystem. Taking consideration of the internal feedback from the vegetation to water table depth, the model simulated a recovery of mosses and a shift of the ecosystem to a different state that was dominated by graminoids and mosses. Modifying the colonized canopy structure to a co-occupied canopy structure in the model enhanced the competition among graminoids and shrubs and simulated a shift of the bog to a shrub colonized system. The results suggested that the alternative steady state of a bog affected by N deposition can differ greatly as it is determined by the dominant feedback loops that merge from all disturbances from climatic drivers and nitrogen deposition. Quantifying the relative importance of these drivers to the competition among PFTs is necessary for improving the predictions on the vegetation the C and N cycling of the system. Canopy structures with a higher organizational complexity than the colonized structure are recommended for modeling plant competition on the plant functional type level in bogs.

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# Synthesis and outlook

## The PEATBOG model

A central product of the doctoral research reported in this thesis is a new dynamic biogochemical model for analyzing N induced change in the C and N cycling in peatland ecosystems. The model consistently integrates the water, soil and vegetation dynamics in peatland ecosystems. Novel features are, among others, the high belowground heterogeneity in the soil, the stoichiometric controls of the interacting C and N processes and a consistent conceptualization of reactivity of C and N. The model emphasizes mass balance principles and thus allows for systematic analyses of the C and N turnover, fluxes and balances in peatlands. The model generates C and N fluxes and pools in three modeled plant functional types (moss, graminoids and shrubs) and in the peat soil and water at 5 cm resolution on a daily time step.

The model simulated the C and N fluxes and pools in the business-as-usual N deposition scenario and a range of N fertilization scenarios that were chosen according to long-term ecosystem experiments at the Mer Bleue Bog, Ontario, Canada, that provided data needed to test and validate the model. The simulated results captured much of the observed vegetation dynamics and most of the changes in the C and N fluxes and pools in the control and the N(PK) fertilized plots in the Mer Bleue Bog from 2000 to 2008. The model suggested a shift of vegetation from dominance of shrubs and mosses to grasses with some remaining shrubs and subsequent changes in ecosystem functioning at extremely high N deposition at 6.4 gN m-2yr-1**.** This result broadly matches the empirical patterns (Juutinen et al., 2010). Some deviations from measurements were visible as well, however. The decline in mosses, for example, was slower than observed plots where eight years of fertilization had nearly eliminated them in the 10N(PK) and 20N(PK) plots (Juutinen et al., 2010). The discrepancies between the simulation and the observation may be explained partially by the differing initial C pools used in the model and in the experimental plots. Other factors that may have contributed to the discrepancies are the model parameterization and the fertilization regime. Examining these factors, the modeling analyses contributed to the clarification the mechanism of the N induced changes occurred empirically. Long-term simulations for the N fertilization scenarios predicted the potential changes in vegetation and the ecological functions of the ecosystem until 2080.

## Key findings

The most crucial finding from the modeling analyses is the importance of vegetation dynamics, as represented by the three most important plant functional types, for C fluxes in northern peatlands. The results showed that the dynamics of these plant functional types responds non-linearly to environmental controls and may show different stable states under similar conditions. The differing stable states of the vegetation will lead to very different functional changes of a simulated peatland in terms of carbon fluxes and sequestration. Probing a range of possibilities of the uncertain parameters, the carbon fluxes deviated along two possible paths that were characterized by dominance of different plant functional types. A graminoid-dominated peatland was characterized by high GEP, ER and NEE and a shrub-moss dominated peatland has smaller GEP, ER and NEE. In the graminoid-dominated peatland, a shift from C gain to C loss was predicted by the model after centuries of fertilization and in only in the scenario with 6.4 gN m-2 yr-1. Such a deposition level is beyond realistic N deposition in nature. The modeling results thus suggested functional changes towards a larger C sink of the peatland ecosystem conceding that graminoids would be promoted by the N enrichment. In contrast, in the shrub-moss dominated peatland type, a net C loss occurred within 20 years after the fertilization began. This result implied some risk of net C release to the atmosphere when shrub-mosses prevail as the dominant plant functional type in the system.

The modeling study revealed some potential causes of the structural and functional changes of peatlands that were examined with respect to consequences of nitrogen deposition. The modeling analyses identified parameters that are currently uncertain and require further empirical investigations to minimize uncertainties in our predictions. One of the parameter that was explicitly tested in this study was the response of photosynthetic capacity to the N content in vascular plants. By modifying the photosynthetic capacity – N content from linear to unimodal in vascular plants in the model, the inhibition from vascular plants on the growth of mosses was reduced and the presence of mosses was sustained in the high N load scenario with 6.4 gN m-2 yr-1. Vascular plants in peatlands are highly adapted to the nutrient poor environment in peatlands by N conservative strategies, such as slowing their growth rates and minimizing leaf for nutrient retention (Small, 1972;Aerts, 1990;Freschet et al., 2010;Eckstein et al., 1999;Grime, 1977). The modeling results suggested that depending on the adaptability of plants to the abrupt changes in the nutrient availability, such as raising the photosynthetic capacity with N accumulating in the tissue as discussed in Chapter 3, the vegetation and the state of the newly adapted system can be disparate.

The second finding that I would like to highlight is the outcome that peatlands are sensitive to both the concentration and the load of N deposition. The model simulated that the N retention of peat and N export from the ecosystem increased with N load and decreased with N concentration. The model predicted an extinction of mosses only when N deposition occurred with a high concentration and load, analogous as employed in fertilization experiments. The suppression of mosses by N fertilization was mitigated by daily deposition of N at low concentrations. Vice versa, the detrimental effect of N deposition on mosses might occur at a low N load with a high concentration in bogs, as has been the case in many fertilization experiments. These results underscore the importance of considering concentration in addition to the load of N deposition when assessing the impact on vegetation and N retention in bogs.

Finally, PEATBOG as a dynamic system model allows for analyses of the dynamic behavior of the peatland ecosystem. The dynamics of the C and N pools and fluxes showed time lags up to approximately 20 years to N deposition before approaching new steady states. The stability of the C and N pools decreased during the first 20 years of the adjustment of the ecosystem. Therefore, observed trends in short-term experiments may have been “snap shots” of the enlarged fluctuation of the ecosystem during the initial adaptation phase to the new environment and, thus, may not easily be extrapolated to longer time periods beyond the actual experiments.

The model predicted a large range of possibilities of the plant functional type composition and the alternative state of the system with N deposition, especially in the context of climate change. Multiple stressors appear to limit the resilience of the bog ecosystem and likely increase the risks of regime shifts (Paine et al., 1998;Turetsky et al., 2012). This modeling study simulated the regime shift of the peatland under two stressors: excessive nitrogen deposition and drought. When the effects of multiple stressors on the system are counteracting, the relative effectiveness of each determines the dominant feedback loop that merges and the final state of the ecosystem, as represented by state variables and process rates. As local climatic conditions vary and responses of site-specific species to each driver differ across peatlands (Bertness and Ewanchuk, 2002), the response of a peatland ecosystem to nitrogen deposition can be very different, as has been observed empirically as well. The results highlighted the need for quantifying the relative importance of multiple disturbances systematically to predict the potential shift of state a peatland ecosystem to N deposition in a changing environment.

## Model prospects and challenges

As a dynamic model that serves the purpose of understanding the mechanisms of complex phenomena in nature (Hall and Day, 1977), the PEATBOG model successfully simulated the observed patterns in nitrogen polluted bog systems and contributed to our understanding of the causes of those patterns. The simulations conducted in this study showed satisfying realism and precision of the model. Further improvement towards realism and precision can be achieved by increasing functional representation of the vegetation in the model. This study showed that the inflexible canopy structure of bog plants in the model omitted potentially important aspects regarding the adaptation of plants to nitrogen. These aspects may not be important in modeling the total biomass of the ecosystem, as was the case in this modeling study, but they are essential for the competition among plant functional types in bogs, as well as the carbon fluxes and carbon sequestration in the ecosystem. The co-limitation of energy and nutrient in systems such as bogs favor plants that are able to adapt to the multiple stressors (Grime, 1977). However, the inevitable trade-offs among plant traits for the adaptation to the multiple stressors (Reich et al., 2003;Wright et al., 2005) result in non-linear responses of the plant community and the ecosystem to multiple stressor (Suding et al., 2008). For peatlands, climatic drivers and nutrient stresses yield effects on a similar magnitude in changing the vegetation and the ecosystem functions. For example, a meta-analysis showed the effect of each 1 degree of temperature increase was comparable to an experimental application of 4gN m-2 yr-1 in depressing the growth of *Sphagnum* (Limpens et al., 2011). Higher organizational complexities of model structure, such as differentiating old and new plant parts and functional components within plants to represent partitioning and growth strategies (Xu et al., 2012) and the morphological and physiological adaptations of plants, are desired for more insightful simulations.

Generality is by definition a contradictory considerate to the other two criteria: realism and precision (Levins, 1966). The PEATBOG model was developed based on fundamental laws to achieve generality. For unavailable parameter values, either assumptions or calibrations were made based on historical data (Table 2.3) from 1999 to 2004. The model was evaluated with data from the fertilized plots that was different from the origin of the historical data from a micrometeorological tower nearby that was used for testing and calibrating the model. Nevertheless, as the two sets of data were from the same bog system, the generality of the model evaluation is limited. Further applications of the model to other bogs are required to evaluate the generality of the model. The inputs required to model other bog systems are confined to climatic records (daily precipitation, photosynthetic active radiation, snow depth and air temperature), nitrogen deposition, the initial vegetation composition and some geographic information (e.g. slope of the site, geographic location) and peat properties (e.g. bulk density, peat porosity).

As a model build in STELLA, the PEATBOG model is advantageous in the easy integration of other processes into the current model. The high spatial resolution belowground and the plant functional type structure in the current structure provide platforms for incorporating other belowground processes and plant types into the system. One potential development of the model could be dividing the pools of electron acceptors, such as SO42-, according to soil layers to explicitly model CH4 dynamics. Although CH4 emission was not a focus for the purpose of this study, the CH4 production was genuinely modeled from an electron competition perspective, which hold promise for future analyses of CH4 dynamics. Another type of further development could be including new plant functional types, such as trees, for a potential application to bogs that are characterized by invasion of trees, for example after drainage, or by death of trees under wetter conditions. In addition, this process-based model provided a mature platform with model components that can be potentially disintegrated and used separately in STELLA to serve other purposes of studies for peatland ecosystems. Some challenges remained though, for the application and developments of the model. First of all, calibration and validation are needed for each application to another bog system. Secondly, large number of parameters and the complexity of the model lead to difficulties in calibrations.

Furthermore, the PEATBOG model is potentially a useful tool for studying the combined effects of climate change and nitrogen deposition. Although this study focused on the impact of nitrogen on peatlands, the PEATBOG model was designed to be sensitive to changes in N deposition, temperature and precipitation. The sensitivity analyses (Chapter 2) demonstrated the adequate sensitivities of the C and N cycles to the change of environmental drivers in addition to nitrogen deposition. This fact shows the prospects of the model for predicting the response of bog ecosystems to nitrogen deposition under a changing climate.

## Summary

Peatlands support unique plant communities and important ecological functions and play a crucial role in regulating the atmospheric carbon budget and maintaining the climate. Fertilizer use and fossil fuel combustion has raised atmospheric nitrogen (N) deposition since the 19th century and have induced ecological changes in peatlands over the last century. Shifts in vegetation and changes in carbon (C) and nitrogen fluxes have been observed empirically, but agreements have not been reached regarding the tolerance of peatland vegetation to N deposition and the extent of the N-induced changes in the functioning of the peatlands in the long-term. To provide a platform answering those questions, the PEATBOG (Pollution, Precipitation and Temperature impacts on peatland Biodiversity and Biogeochemistry) model was developed to simulate the interacting C and N cycles in peatlands. The new dynamic model was designed using a systems approach, aiming to track the C and N throughout the system from a biogeochemical perspective.

The PEATBOG model consists of four sub-models, which simulate the soil environment, plant growth and competition between three plant functional types, peat decomposition and soil water chemistry. The model is the first process-based model that both incorporates plant competition and ensures integrity of the C and N cycle. It is novel in the integration of processes and sub-systems, the focus on the heterogeneity of the belowground environment in peatlands and the consistency in the mass balance and material reactivity concept within the peatland. The model was tested to be adequately sensitive to nitrogen pollution, precipitation and temperature for a potential incorporation of the climate change effects into the analysis.

A model evaluation showed realistic and precise simulations of the nutrient-induced changes observed in the nutrient addition experiments in the Mer Bleue Bog in Canada. The model simulated the vegetation shifts of peatlands from shrub-moss dominated to graminoid-dominated with highly elevated N deposition. The results revealed a strong link between vegetation and the magnitude of C fluxes and the potential structural and functional adaptation of the ecosystem to nitrogen deposition. The simulation showed that the peatland remain a C sink with graminoids dominated the system, but can also switch to a C source when shrubs and mosses prevailed in the system. The findings also highlight the impact of both N load and N concentration on the vegetation and carbon and nitrogen cycling. Both factors need to be considered when effects on peatlands are evaluated. A potential risk to peatlands, particularly to *Sphagnum* mosses, may also occur when low N loads are low but N concentration high in the precipitation or in water mosses are exposed to. Long-term predictions using the model suggested differing possibilities regarding the plant composition and the state of the ecosystem under stress by N deposition, especially when combined with climate change. More realistic representations of the plant canopy structure are needed for the model to take care of the nutrient investment and physiological and morphological adaptations of the plants. The study demonstrated the usefulness of the PEATBOG model for understanding and conceptualizing observed patterns in C and N cycling in peatlands, for analyzing the mechanisms involved, for identifying critical gaps in our empirical knowledge and potentially for building hypotheses. In addition, the user-friendly model structure provides a platform for integrating other processes into the model and opens various possibilities for further applications for future biogeochemical research in bogs.

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