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The fate of ^{15}N-nitrate in mesocosms from five European peatlands differing in long-term nitrogen deposition rate

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Abstract

Elevated nitrogen (N) deposition changes the retention, transformation, and fluxes of N in ombrotrophic peatlands. To evaluate such effects we applied a ^{15}N tracer ($NH_4^{15}NO_3$) at a rate of 2.3 g N m^{-2} yr^{-1} to mesocosms of five European peatlands with differing long-term N deposition rates for a period of 76 days of dry and 90 days of wet conditions. We determined background N content and moss length growth, and recovered the ^{15}N tracer from the mosses, graminoids, shrubs, the peat, and dissolved N. Background N contents in *Sphagnum* mosses increased from 5.5 (Degerö Stormyr, deposition < 0.2 g N m^{-2} yr^{-1}) up to 12.2 mg g^{-1} (Frölichshaier Sattelmoor, 4.7–6.0 g N m^{-2} yr^{-1}). In peat from Degerö nitrate and ammonium concentrations were below 3 mg L^{-1}, whereas up to 30 mg L^{-1} (nitrate) and 11 mg L^{-1} (ammonium) was found in peat from Frölichshaier Sattelmoor. *Sphagnum* mosses (down to 5 cm below surface) generally intercepted large amounts of ^{15}N (0.2–0.35 mg g^{-1}) and retained the tracer most effectively relative to their biomass. Similar quantities of the ^{15}N were recovered from the peat, followed by shrubs, graminoids and the dissolved pool. At the most polluted sites we recovered more ^{15}N from shrubs (up to 12.4 %) and from nitrate and ammonium (up to 0.7 %). However, no impact of N deposition on ^{15}N retention by *Sphagnum* could be identified and their length growth was highest under high N background deposition. Our experiment suggests that the decline in N retention at levels above ca. 1.5 g m^{-2} yr^{-1}, as expressed by elevated near-surface peat N content and increased dissolved N concentrations, is likely more modest than previously thought. This conclusion is related to the finding that *Sphagnum* species can apparently thrive at elevated long-term N deposition rates in European peatlands.

1 Introduction

Peatlands, as important carbon (C) stores, have accumulated approximately 615 GtC since the Last Glacial Maximum (Yu et al., 2010). Their carbon uptake can be altered by hydrological, climatic and human-induced factors, such as groundwater level change (e.g. Blodau et al., 2004; Deppe et al., 2010; Moore and Knowles, 1989), temperature fluctuations (e.g. Daulat and Clymo, 1998; Lafleur et al., 2005) or elevated nitrogen (N) deposition (e.g. Bragazza et al., 2006; Juutinen et al., 2010; Keller et al., 2005). Increase in N concentrations, a key growth-limiting nutrient in peatlands (Aerts et al., 1992), can cause changes in vegetation composition (e.g. Heijmans et al., 2001; Juutinen et al., 2010; Wu et. al. 2015) and promote biodiversity loss (Dise et al., 2011).

Ombrotrophic peatlands are exclusively fed by rain water and especially sensitive to atmospheric N inputs. Over the last century many of these ecosystems have received inputs of atmospheric N deposition even ten-fold larger than the pre-industrial levels (van Aardenne et al., 2001). In Europe, where N deposition strongly varies spatially, the mean change in N deposition between 1950–2000 and 1900–1950 was between 0.4 and 1.6 $\mathrm{g\,m^{-2}\,yr^{-1}}$ (Granath et al., 2014). Although the future estimates of N emissions (NO_x and NH_3) vary, with some indicating a substantial further increase (Galloway et al., 2004) and others suggesting stabilization or even slight decrease of emissions by 2030 given an appropriate emission control (Cofala et al., 2007), the importance of elevated N inputs to peatlands remains undisputable.

Elevated N supply has been documented to cause various shifts in peatland N cycling such as a decrease of C : N ratio in near surface peat (Bragazza et al., 2012), stimulation of denitrification (Francez et al., 2011), and an increase of N concentration in interstitial waters (Limpens et al., 2003). It has also been reported that plant community change from *Sphagnum*-dominated to vascular-dominated and the enhanced N inputs may turn peatlands into C sources (Bubier et al., 2007; Wiedermann et al., 2007). The effect of N deposition on the retention ability of *Sphagnum* mosses is also dependent on N deposition rate. At low N deposition levels the growth of *Sphagnum* can be promoted (Aerts et al., 1992), which suggests that also N retention is raised. At high N deposition, however, *Sphagnum* was found to lose its filtering capacity (Lamers et al., 2000; Limpens and Berendse, 2003). As a result elevated N input to ombrotrophic peatlands and declining uptake by *Sphagnum* could potentially enhance denitrification due to increased N availability in the pore waters of affected systems (Hayden and Ross, 2005).

A quantification of N transformation rates and fluxes under conditions of varying long-term N deposition is crucial for understanding the mechanisms and robustness of N retention. Several experimental studies have addressed the impact of increased N deposition on the functioning of peatland vegetation (e.g. Aldous, 2002a; Curtis et al., 2005; Williams et al., 1999b). Lower N retention in the upper stem moss tissue (Aldous, 2002b) and higher N_2O emissions (Regina et al., 1996) have been documented with decreasing water table. However, to our knowledge, the fate of N in peatland ecosystems under varying N inputs and hydrological conditions has not been examined extensively yet (Blodau et al., 2006; Xing et al., 2010). Studies on the fate of N within moss, vascular plants, and upper peat layer, including the pore water, are needed in light of the already mentioned expected elevated N emissions. In this contribution, we investigate how the allocation of N in plants and peat is altered under different N pollution levels using ^{15}N labeled nitrate. We conducted a controlled mesocosm experiment with intact peat cores, including the vegetation, from five European peatlands, which have a history of differing long-term N deposition. This gradient approach allowed us to avoid the shortcomings of short-term fertilization studies, in which the time scale of manipulation is generally too short for an adjustment of ecosystem structure and functioning. Labeled N was used to investigate how the allocation of N in plants and peat was altered under the different long-term N pollution levels the sites were exposed to. We hypothesized that the sites with a legacy of low N deposition would experience low mobility and high retention of N in vegetation and near-surface peat, whereas the sites with a legacy of higher N deposition would experience high mobility and low retention

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of the element. We further expected nearly complete absorption of the applied ^{15}N by *Sphagnum* at low background N deposition, and diminished absorption by mosses and raised uptake by vascular plants at background N deposition exceeding levels of about 1.0–1.5 $\mathrm{g\,N\,m^{-2}\,yr^{-1}}$ (Bragazza et al., 2006; Lamers et al., 2000).

In particular we examined:

1. transformation pathways of N within the peat soil, e.g. from inorganic N to organic N and from nitrate to ammonium,
2. differences in N transformation in relation to the legacy of atmospheric N deposition, and
3. whether mosses from “clean” sites would be able to assimilate N more efficiently than mosses from “polluted” sites.

2 Materials and methods

2.1 Study sites

We selected five *Sphagnum*-dominated peatlands in Northern and Western Europe: Degerö Stormyr (DS), Sweden; Lille Vildmose (LV), Denmark; Fenn’s Whixall and Bettisfield Mosses NNR (WM), UK; Cors Fochno (CF), Wales, UK; and Frölichshaier Sattelmoor (FS), Germany. The differences in the soil acidity between the sites were small – pH ranged between 3.6 and 4.0 and was typical for ombrotrophic peatlands (Rydin and Jeglum, 2006). Site specific characteristics as well as the typical vegetation are presented in Table 1.

2.2 Experimental design and sampling

In the summer of 2009 we collected three intact peat monoliths (“cores”, “mesocosms”, 30 cm in diameter, 40 cm long) from lawns of the five sites. This resulted in 15 meso-

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cosms, which were subsequently incubated in a greenhouse chamber at 20 °C, c. 60 % rH, and were exposed to 12h light/dark cycles. Directly after collection, all mesocosms were drained and then rewetted to a water table of 28 ± 3 cm below the moss layer. The experiment commenced in November 2009, after a two to three month (depending on the collection date) acclimation period. During the first 76 days all mesocosm were subjected to low water table level (−28 ± 3 cm), here also called "dry period". Between day 77 and 78 we raised the water level up to ca. −8 cm using deionised water and maintained it there (±3 cm) for the next 90 days, until the end of the experiment in the middle of April ("wet period").

Mesocosms were watered twice a week using a self-made sprinkler. During the acclimation period we added a synthetic rainwater solution, whose chemical composition was based on the average European rainwater composition (Appelo and Postma, 2005), with N concentrations adjusted for each site. Specifically, the concentrations were 16.65 mg L^{-1} $NH_4^{15}NO_3$, and 2.94 ($CaCl_2 \cdot 2H_2O$), 1.63 (MgCl), 3.70 (Na_2SO_4), 0.52 (K_2SO_4), 0.029 (H_2SO_4) and 0.002 (HCl) mg L^{-1} during the experiment. In the acclimation period N deposition differed between sites and was adjusted to 1.57 (DS), 6.26 (CF), 9.39 (WM), 12.53 (LV) and 16.44 (FS) mg L^{-1} NH_4NO_3. Throughout the experiment (November–April), we substituted NH_4NO_3 in the irrigate with the $NH_4{}^{15}NO_3$ tracer at 2.3 g of N $\text{m}^{-2}\,\text{yr}^{-1}$ (1.1 g of N added over the experimental period) to each mesocosm. This deposition level was found by Blodau et al. (2006) to be almost fully absorbed by mosses in mesocosms from unpolluted sites, whereas breakthrough of the tracer was expected in mesocosms from N polluted sites. The ^{15}N application thus allowed us to trace the fate of N in peat cores exposed to different background N-deposition levels. The remaining rainwater solution stayed unchanged. When referring to the "start" and the "end" of the experiment we refer to the first ^{15}N tracer application and the sampling following the last ^{15}N application, respectively.

Throughout the experiment, we recorded the water level in all mesocosms twice a week, and adjusted it when necessary. Peat soil moisture (SM) content was logged hourly (ECH_2O EC-5 FD sensors, Em5b loggers, Decagon Devices Inc.) at 4 depths

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in one core from each site. We calibrated the sensors for each site and for the top and the bottom of the peat core (see Supplement). Polynomial equations ($R^2 > 0.82$) were used to calculate the volumetric water content at 1 h time steps.

Sampling of peat water and gas was performed fortnightly. The extracted gas volume was replaced with nitrogen gas (N_2) at each sampling depth. Gas flux from the mesocosm surface was measured during 20 min long sampling period, including 5 sampling points in 5 min intervals. We used plexiglas chambers (27 cm in height and 29 cm in diameter) with an inlet and outlet tube at the top. The peat water was sampled using Rhizon® samplers (polymer, 1 µm pore size, Eijkelkamp Agrisearch Equipment) at 4 depths: 9, 16, 23 and 30 cm below the *Sphagnum* surface and through the PE cord from the bottom of each core. The pH of peat water was measured immediately using a glass electrode. The water samples were stored cool, or frozen for later analyses.

The length growth of *Sphagnum* moss community was measured in all mesocosms using three cranked wires (Clymo, 1970) per mesocosm. Wire lengths were measured shortly after installing, in the middle and in the end of the experiment. Single species of *Sphagnum*, shrubs and graminoids designated for isotopic analyses were sampled from each mesocosm at the end of dry and at the end of wet period. Plant samples used for estimation of background ^{15}N contents were collected directly from the sampling sites.

After termination of the experiment in April 2010 total aboveground biomass was quantified from each core. We clipped the whole plant material from the mesocosms' surface, distinguishing between main plant functional types (shrubs, graminoids and mosses). Mosses were collected down to 5 cm below the moss canopy. After the biomass collection, we then sequentially extracted the pore water from individual depth layers through the gas sampler openings. The extraction continued from the top of the core downwards until no water from the single layer could be obtained. Due to a large water volume required for the ^{15}N analysis and differences in a field capacity between the cores and specific peat layers, it was not possible to obtain exactly the same layer depths for all mesocosms. At last, the cores were extracted and one part of each core cut into 2–8 cm (higher resolution at the top and lower at the bottom) segments for ^{15}N analyses. The remaining parts were used for bulk density (BD) estimations. The peat for background ^{15}N measurements was collected before the first tracer application using a stainless steel microcorer (3 cm in diameter).

All organic samples were dried at 70 °C for at least 24 h or until no more mass loss could be recorded. The samples used for aboveground biomass and bulk density estimation were then weighed and the samples destined for isotopic analysis were ground with a ball mill to fine powder and stored in an evacuated desiccator prior to analysis.

When reporting sampling depths, we report the depth relevant not to the rim of the mesocosm tube but to the *Sphagnum* surface, thus obtaining discrepancies of up to 1 cm between the cores.

2.3 Chemical analyses

We measured nitrate (NO_3^-) concentrations by ion chromatography (Metrohm IC 733 with suppressor module, Metrosep Dual 3 column). Ammonium (NH_4^+) concentrations were quantified photometrically at 690 nm (ISO 7150/1) on a DR 3800 photometer using NH_4^+ quick test method (Ammonium test, range: 0.01–3.00 NH_4-N mg L^{-1}, Merck). Total dissolved N (TDN) and particulate N (PN) were measured on a TOC/TN analyzer (multi N/C 2100, Analytik Jena, NPOC analysis). Dissolved organic N (DON) concentrations were calculated as the difference between TDN and dissolved inorganic N (DIN) (NO_3^- plus NH_4^+). Nitrous oxide (N_2O) samples were measured on a Varian gas chromatograph with flame ionization (FID) and electron capture (ECD) detectors. We did not detect any N_2O flux from the mesocosms throughout the duration of the experiment.

2.4 Isotopic analyses

The ratios of natural abundance and tracer $^{15}N/^{14}N$ as well as total C and N were quantified in the dried plant material and the peat using an elemental analyzer (NA 1108 –

natural samples, NC 2500-labeled samples, CE instruments, Milano, Italy), connected via ConFlo III interface to a delta S/delta plus IRMS (natural/labeled, Finnigan/Thermo Fisher Scientific, Bremen, Germany). Dissolved inorganic ^{15}N content in pore water samples was assessed by a sequential trapping of volatilized NH_4^+ and NO_3^- (Brooks et al., 1989) – procedure modified and described in detail in Blodau et al. (2006).

High purity of the added tracer (98 atom% ^{15}N) and high frequency of watering events resulted in extremely high isotopic signatures of most peat and plant samples, exceeding the calibration range of the instrument. We thus diluted all samples with a natural plant material of known ^{15}N content and remeasured the samples. Comparison of the two data sets revealed a close correlation ($y = 0.9623x + 0.0036$, $R^2 = 0.71$, see Supplement, Fig. S1). For interpretation we thus used the original ^{15}N data set.

The ^{15}N results were expressed as % content of ^{15}N atoms in total N atoms (atom% $^{15}\text{N} = [^{15}\text{N}/(^{14}\text{N} + ^{15}\text{N})] \times 100\,\text{atom\%}$). The ^{15}N abundances (atom% ^{15}N excess) were obtained by subtracting the background ^{15}N of plants, peat and traps (diffusion procedure) from the labeled samples.

2.5 Data handling and statistical analyses

We calculated area-based plant biomass, peat density and total nitrogen (TN) content of the ecosystem pools as well as volume-based ^{15}N content in peat and plant pools. Additionally, ^{15}N retention efficiency and ^{15}N recovery from the pools was estimated. The relative share of each of the ecosystem pools to the total ^{15}N recovered (%) was obtained by dividing their tracer mass by the total mass of the tracer added to the system. The sum of the relative shares of each pool gave the total ^{15}N recovery.

Statistical analyses were performed with the SPSS 20.0 package and SigmaPlot for Windows, version 11.0. The effect induced by differing long-term N deposition (sites) on N pools and ^{15}N retention and of wet and dry conditions on ^{15}N uptake by plants was analyzed by one-way analysis of variance (ANOVA) followed by a post-hoc test (Tukey or Bonferroni). Uptake of ^{15}N was additionally analyzed by a paired *t* test. Significance was set at $p \leq 0.05$, unless stated otherwise.

Before reporting the results of N concentration measurements, a few words on the uncertainty in data are needed. We encountered an issue when evaluating the pore water concentration data from FS cores – NO_3^- concentrations in the first part of the experiment were by far exceeding the measured TDN concentrations. A re-measurement of the problematic samples did not give a solution to that problem. Thus, the DON data for the first 98 days needed to be omitted, otherwise showing negative values.

3 Results

3.1 Nitrogen contents

Weight based (Fig. 1) and area based (Fig. 2) N contents differed between the sites, albeit often not significantly. The average N content of peat, plant and dissolved pools, expressed as the ratio of the mass of N present in the pool to the total mass of the pool, generally increased along the N deposition gradient (Fig. 1). Surface peat layer (5–15 cm depth) contained between 5.3 ± 0.3 (DS) and 13.4 ± 2.3 (CF) $\mathrm{mg\,N\,g^{-1}}$ and this difference was significant. *Sphagnum* (capitulum and stem) and shrubs had similar N contents varying between 4.9 ± 2.5 and 9.8 ± 3.9 $\mathrm{mg\,g^{-1}}$, and 5.7 ± 0.8 and 10.7 ± 1.7 $\mathrm{mg\,g^{-1}}$ respectively. The N content in *Sphagnum* was generally higher in the apical part than in the stem part and ranged between 5.6 ± 0.5 (DS) and 12.2 ± 6.4 (FS) $\mathrm{mg\,N\,g^{-1}}$ (Fig. S2). We recorded a very high shrub N content at Degerö Stormyr resulting from high N content of *Andromeda polifolia* leaves at this site (Fig. 1). Graminoids were the most N-rich plant functional type (8.4 ± 1.5 –18.9 ± 4.0 $\mathrm{mg\,g^{-1}}$) and their N content differed significantly ($F(4,10) = 8.099$, $p = 0.004$) between Frölichshaier Sattelmoor and the rest of the sites. The least N was found in the dissolved pool (Fig. 1). Total dissolved N content in the surface layer of peat (0–15 cm) ranged from 1.95 ± 0.12 to 6.17 ± 1.27 $\mathrm{\mu g\,g^{-1}}$ and differed significantly between LV cores and DS and WM cores ($F(4,10) = 5.82$, $p = 0.01$). ANOVA further showed that N content in the ecosystem pools significantly differed from each other; the post-hoc test indicated that at the level

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of sites the differences between graminoids, *sphagnum* and shrubs were significant at the DS site ($p = 0.002$ and $p = 0.018$) and FS site ($p = 0.01$ and $p = 0.001$). Significant differences also occurred between graminoids and peat (DS, FS, CF), and shrubs and *sphagnum* and peat (CF).

Area based N content of ecosystem pools, calculated by multiplying biomass (plants), bulk density (peat) or volumetric water content (Supplement, Table S1) with N content, varied between the sites but the differences were mostly not significant (Fig. 2). Due to its large mass, peat contained by far the largest N pool and held between 22.8 ± 4.6 (DS) and 63.5 ± 11.5 (CF) $\mathrm{g\,N\,m^{-2}}$ in the 10 centimeter subsurface layer. *Sphagnum* moss constituted the second largest N pool and contained between 4.0 ± 0.8 (WM) and 9.0 ± 0.3 (LV) $\mathrm{g\,N\,m^{-2}}$. Total N content was similar for shrubs and graminoids varying between 0.6 ± 0.16 and 2.8 ± 0.61 $\mathrm{g\,N\,m^{-2}}$ and between 0.4 ± 0.25 and 1.7 ± 2.07 $\mathrm{g\,N\,m^{-2}}$, respectively. The N content in these two plant functional types was highest at Frölichshaier Sattelmoor (Fig. 2), and statistically differed from that of the DS site. Lowest TDN values were detected at low long-term N deposition for shrubs and at intermediate long-term N deposition levels for graminoids (Fig. 2). The dissolved pool contained the smallest quantities of N. Total dissolved N content increased along the N deposition gradient and ranged from 0.03 to 0.63 $\mathrm{g\,N\,m^{-2}}$ (Fig. 2). The largest amounts of TDN were found in the LV site and differed significantly from both DS and WM (Fig. 2).

3.2 Nitrogen uptake by plants

Uptake of ^{15}N varied between plant functional types and was additionally influenced by water table position. The highest ^{15}N enrichment was observed in the *Sphagnum*'s apical part, followed by *Sphagnum* stem, shrubs and graminoids (Fig. 3). Tracer uptake by the capitulum of *Sphagnum* was significantly elevated during the dry period and declined after the water table was raised (Fig. 3a), as confirmed by One Way ANOVA ($p < 0.002$). The enrichment with ^{15}N in *Sphagnum* (0–5 cm) decreased along the long-term N deposition gradient, with Degerö Stormyr having highest and Frölichshaier

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Sattelmoor smallest uptake during the dry period at 5.9 and 2.9 % in the capitulum, respectively (Fig. 3a). Unlike in *Sphagnum*, the largest ^{15}N enrichment in shrubs occurred during the wet period (Fig. 3c and d). Shrubs assimilated on average twice as much of the tracer during this second part of the experiment (Fig. 3c; One Way ANOVA, $p < 0.001$).

3.3 Retention and recovery of added ^{15}N

To examine the retention capabilities of each of the pools, retention efficiency per gram of dry weight was calculated from the quotient of ^{15}N retained at the end of the experiment divided by dry biomass or dry peat mass, respectively. The sites substantially differed in ^{15}N retention efficiency, when all pools were accounted for, yet differences between sites were statistically significant only with regard to the shrub pool and sites DS and CF, and DS and WM (Fig. 4). Vegetation was up to four times more effective in retaining N than peat and *Sphagnum* moss was significantly more efficient than graminoids and peat ($p = 0.007$ and $p = 0.001$), as were the shrubs ($p = 0.013$). Cors Fochno and Whixall Moss vegetation had the smallest retention efficiency varying between 0.05 ± 0.02 in graminoids (CF) and 0.2 ± 0.06 in *Sphagnum* (0–5 cm) (WM) (Fig. 4). Interestingly, *Sphagnum* from both the sites with low (DS) and the sites with high (LV, FS) level of background N input was equally effective in absorbing N, but peat in LV and FS cores retained substantially less N than the peat in WM cores (Fig. 4).

During the course of the experiment we applied 38 mg (572 mg m^{-2}) of ^{15}N to each mesocosm. After 24 weeks, the recovery, i.e. the mass of ^{15}N divided by amount of ^{15}N added, of the tracer from all N pools ranged from 87.5 to 131 % (Table 2). Recoveries above 100 % were most likely caused by the uncertainty in the peat bulk density. The depth resolution used in ^{15}N sampling (6–8 sections per core) was much higher than the resolution used in the bulk density measurements, which encompassed only 2–3 depth intervals per core. Especially the ^{15}N content in the most upper peat layers, where BD was possibly lower than the average BD of a thicker peat layer, may have been overestimated. *Sphagnum* and peat contained the largest fraction of the tracer and accounted for 21.9 to 68.9 % and 23.6 to 65.6 % of the total, respectively. Vascular plants contained only between 5.6 and 13.6 % of the recovered ^{15}N. The shrubs had an up to thirteen times higher share than the graminoids (Table 2). The shrubs in cores from Frölichshaier Sattelmoor were particularly efficient in retaining the tracer and accounted for 91 % of the retention in vascular plants (Table 2). Dissolved inorganic ^{15}N contributed little to the retention of ^{15}N at levels below 1 % but its share increased with background N deposition rate (Table 2). This pool accounted for 0.01 % (DS), followed by 0.2 % (CF and WM), 0.4 % (FS) and 0.7 % (LV).

3.4 Dissolved nitrogen

The dissolved N concentration increased along the long-term N deposition gradient at the sites (Fig. 5, Table 1). Nitrate was detectable predominantly above the water level but remained low ($< 3\,\mathrm{mg\,L^{-1}}$) in the majority of the cores (Fig. 5). Only in the cores from Frölichshaier Sattelmoor, NO_3^- concentrations reached $30\,\mathrm{mg\,L^{-1}}$ and were especially high during the first 35 days of the dry period. Ammonium concentrations reached $11\,\mathrm{mg\,L^{-1}}$ at the site characterized by high levels of N input (FS) and $2\,\mathrm{mg\,L^{-1}}$ at the site with low level of N input (DS) (Fig. 5). The smallest detectable NH_4^+ concentrations were found at DS and were as low as $0.3\,\mathrm{mg\,L^{-1}}$ at a depth of 30 cm half way through the experiment (Fig. 5). The highest NH_4^+ concentrations were found at FS, 15–20 cm below the *Sphagnum* surface, i.e. ca. 10–15 cm above water level, during the dry period (Fig. 5). Between days 77 and 78 ammonium concentrations declined, which was probably caused by a dilution from wetting, but returned to previous levels within 5 days (Fig. 5). Total dissolved N remained low at the low long-term N deposition sites (DS) and increased substantially in the high long-term N deposition site (FS; Fig. S3a). Higher concentrations were found mainly above the water table (Fig. 5). The concentrations varied from 1.3 to $5.1\,\mathrm{mg\,L^{-1}}$ at Degerö Stormyr and from 2.4 to $17.3\,\mathrm{mg\,L^{-1}}$ at Frölichshaier Sattelmoor. Dissolved organic N also increased along the long-term N deposition gradient (Fig. 5, Table 1). Sites with a legacy of high long-term N deposition (LV, FS) had elevated DON concentrations reaching $5.3\,\mathrm{mg\,L^{-1}}$ (FS), whereas the other sites contained less than 1 mg DON L^{-1}. Particulate N content at the bottom outlet of the cores was between 0.2 and 5 mg L^{-1} (Fig. S3b). The highest PN concentrations, recorded for sites with intermediate and high long-term N deposition levels (WM, LV, FS), were measured during first 15 days and declined substantially thereafter (Fig. S3b). At Degerö Stormyr, PN and TDN contents in the pore water were similar and generally did not exceed 3 mg L^{-1} (Fig. S3). At other sites, PN was on average 20 to 90 % lower than TDN.

3.5 ^{15}N distribution in peat and pore water

The distribution of the experimentally applied ^{15}N in peat was influenced by background N deposition rates and decreased with depth. A sharp decrease of the ^{15}N signal, expressed as the difference between the ^{15}N signal recorded at the end of the experiment and the natural ^{15}N background, was observed between 10 and 15 cm depth and 78–98 % of the total ^{15}N peat pool was retained in the top 20 cm of the peat profile (Fig. 6). The isotopic signal was elevated most at sites with the low and intermediate long-term N deposition levels and reached 4 at% ^{15}N excess in the near-surface peat (Fig. 6a) at the end of the experiment. At sites with high long-term N deposition rates, on the contrary, the amount of ^{15}N in excess of the background was much lower – in a range of 0.2–0.6 at% in the top layers (Fig. 6a). The mean values oscillated between 0.28 (LV) and 1.95 (DS) at% ^{15}N excess. Volume based ^{15}N content in peat was calculated by multiplying the experimental isotopic signal of the ^{15}N content in peat layers by their bulk density, and the pattern was similar to the distribution of the isotopic signal (Fig. 6b).

The isotopic signal in pore water was coupled to the ^{15}N distribution in the peat, as contents decreased both with depth and background N deposition (Fig. 7a and b). The ^{15}N-NO_3^- and ^{15}N-NH_4^+ concentrations were only in FS cores lower than expected, which was most probably a result of dilution with abundant, unlabelled dissolved N at this site. The ^{15}N excess in nitrate was similar among sites (Fig. 7a), but it substan-

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tially differed regarding ammonium (Fig. 7b). Volume-based dissolved inorganic ^{15}N content – the product of DIN concentration, volumetric water content and at% ^{15}N-DIN excess – differed significantly (Kruskal–Wallis, $p < 0.001$) between nitrate and ammonium but not between sites (Fig. 7c and d). The differences mostly resulted from the discrepancies in concentrations between these two N species (Fig. 5). The ammonium concentration was up to 100 times higher than the corresponding nitrate concentration. Concentration of $^{15}\text{N-NH}_4^+$ generally decreased with depth, whereas $^{15}\text{N-NO}_3^-$ did not show any specific pattern and remained at low levels at Degerö Stormyr, Cors Fochno and Whixall Moss, with exception of the bottom layer (Fig. 7c and d).

A more detailed examination of the individual cores from Degerö Stormyr (low background N deposition) and Frölichshaier Sattelmoor (high background N deposition) revealed two patterns of the dissolved $^{15}\text{N-NH}_4^+$ distribution in the peat (Fig. 8). Frölichshaier Sattelmoor had up to tenfold larger at% ^{15}N excess than Degerö Stormyr (0.036–0.349 at% $^{15}\text{N-NH}_4^+$ excess and 0.002–0.045 at% $^{15}\text{N-NH}_4^+$ excess respectively). The $^{15}\text{N-NH}_4^+$ concentration decreased gradually with depth in the FS cores, but peaked between 16 and 21 cm below the surface in the DS replicates (Fig. 8).

4 Discussion

4.1 Nitrogen transfer within the mesocosm system

The aim of this mesocosm study was to characterize changes in the transport and transformation of N within ombrotrophic peatlands that are induced by long-term N deposition. We are aware that we did not address all aspects of N pools and transformations – uptake of N by microorganisms and transfer of ^{15}N into DON were, for instance, not investigated. Nevertheless, the results at hand provide some insight into the fate of N entering in the form of nitrate under varying long-term N deposition rate. While the basic pattern of N distribution appeared to stay intact, the quantitative distribution of the ^{15}N tracer between the mesocosm pools differed depending on the background

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N inputs. We found a decline of N recovery from the peat pool and an increase of N recovery from shrubs and the dissolved pool across the N deposition gradient (Table 2, Table 1). A similar change in the N recovery of added ^{15}N-nitrate was observed by Xing and others (2010) after 7 years in a nutrient fertilization study at the Mer Bleue bog, where controls and treatments were fertilized with 1.6, 3.2 and 6.4 $\mathrm{g\,N\,m^{-2}\,yr^{-1}}$ applied in 7 doses during the vegetation period. The retention efficiency of peat and vegetation pools was furthermore lowest in the mesocosms from the sites characterized by the intermediate long-term N deposition levels (Fig. 4), which is in conflict with expectations. Curtis and others (2005), for example, argued for a retention efficiency peaking at intermediate deposition levels and decreasing towards polluted sites. These results are, however, limited to N deposition in form of nitrate, which is generally the dominant inorganic N source in non-agricultural areas (Galloway et al., 2004), yet may not be the preferred form of N assimilated by mosses (Wiedermann et al., 2009).

The peat not only contained the largest N pool (Fig. 2) but also similar or even more ^{15}N than the moss layer (Table 2), which here was defined to reach down to a depth of 5 cm beneath the moss canopy. This finding is in agreement with a previous mesocosm study performed by Blodau et al. (2006) using peat cores and ^{15}N-nitrate as tracer from the Mer Bleue Bog exposed to approx. 1.6 $\mathrm{g\,N\,m^{-2}\,yr^{-1}}$ and the Experimental Lake Area exposed to approx. 0.3 $\mathrm{g\,N\,m^{-2}\,yr^{-1}}$, and the previously mentioned field study by Xing et al. (2010). A substantial mass transfer of ^{15}N into the peat occurred, although only very little dissolved ^{15}N was recovered (Table 2). Blodau and others (2006) could not explain the N transfer into the peat by solute movement either and speculated that ^{15}N was transported in form of the particulate organic N (PON), which was not analysed in their study. The movement of PON could, to some extent, explain high recoveries of ^{15}N from the peat pool also in this case, although no experimental evidence can be provided. One can speculate that the PN concentrations measured at the bottom outlet of the cores were probably only a fraction of those in the upper layers considering that the highest TDN concentrations were measured between 15 and 25 cm below the *Sphagnum* surface (Fig. 5).

Mosses not only intercepted large amounts of ^{15}N in the mesocosms but they also retained the tracer most effectively relative to their biomass. Since *Sphagnum* serves as an effective filter for inorganic N under unpolluted conditions (Lee et al., 1990), we expected ^{15}N-nitrate to accumulate most strongly in the mosses of Degerö Stormyr (Table 1, Fig. 1), and inorganic N concentration to be very low beneath. The Swedish site was indeed most efficient in retaining N, storing on average 0.25 mg N g^{-1}, mostly in *Sphagnum* (0–5 cm) and shrubs (Fig. 4). We also recovered 65 % of tracer from the Degerö Stormyr *Sphagnum* pool only (Table 2) and measured the highest ^{15}N content in the near-surface peat (Fig. 6) at that site. In line with our hypothesis that N mobility would increase with a legacy of long-term N deposition, particularly above previously found N threshold values of 1.0–1.5 g N m^{-2} yr^{-1} (Bragazza et al., 2006; Lamers et al., 2000), we found polluted sites (LV and FS) to contain the largest dissolved N pools (Fig. 2) and the highest nitrate concentrations (Fig. 5). Nitrate not assimilated by N-rich *Sphagnum* (Fig. 1) leached through the *Sphagnum* layer and entered the rooting zone of the vascular plants. This finding was also reflected in the higher ^{15}N recovery from shrubs with increasing background N deposition (Table 2). Remarkably, however, large amounts of ^{15}N were still retained in the N-rich *Sphagnum* layers. Recoveries of 58 and 45.5 % for Lille Vildmose and Frölichshaier Sattelmoor respectively, were in the range of the recovery recorded for the *Sphagnum* layer (0–5 cm) from Degerö Stormyr. This finding shows that under N-rich conditions *Sphagnum* mosses can still filter inorganic N, most likely by the ongoing formation of new biomass, which continuously requires N. It also confirms results of previous studies, where high N deposition rates did not seem to have detrimental effect on *Sphagnum* growth (e.g. Granath et al., 2009; Heijmans et al., 2001; Limpens and Berendse, 2003) and where other aspects such as the presence of vascular plants or climatic factors could potentially affect the mechanisms of N impact on *Sphagnum* production (Limpens et al., 2011). When the plant-peat soil system remains intact and dominated by mosses and shrubs, as was the case across the selected sites, thresholds at which the filter function of *Sphagnum* is entirely lost do not seem plausible.

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The robustness of N uptake by mosses may further be supported by either physiological acclimation or species replacement. We allude that an adjustment to higher N inputs in Lille Vildmose and Frölichshaier Sattelmoor may have contributed to the greater resilience of *Sphagnum* species against enhanced long-term N deposition. The question arises whether (a) high N retention in the N-rich *Sphagnum* layers was a consequence of the ability to better utilize N by fast-growing species (*papillosum* (FS), Table 1) or whether (b) a shift to more tolerant species had occurred. Heijmans and others (2001) found that *Sphagnum* growth during three growing seasons was not limited by high ($5\,\mathrm{g\,N\,m^{-2}\,yr^{-1}}$) levels of N deposition and mosses previously exposed to a background deposition of ca. $1.5\,\mathrm{g\,N\,m^{-2}\,yr^{-1}}$ were still able to assimilate a large portion of experimentally deposited N. The potential ecophysiological adjustment of mosses to an elevated N deposition could evolve, for example, by a gradual increase of the *Sphagnum* tissue N content (Wiedermann et al., 2009). Given that the species in the Lille Vildmose and Frölichshaier Sattelmoor mesocosms differed, it cannot also be ruled out a priori that a shift to different species assisted in maintaining the filtration capacity of *Sphagnum* at these sites. Historical information of Loeske (1903) does not support this idea, however, because in the beginning of the 20th century *S. papillosum* already dominated in the area of Torfhaus, where the Frölichshaier Sattelmoor mesocosms were sampled. Thus, the scenario of species' shift does not seem credible, at least with regard to the Frölichshaier Sattelmoor peatland.

Nitrogen uptake by *Sphagnum* and higher plants was influenced by peat water content. Since there is no mechanism for controlling N uptake in *Sphagnum* (Jauhiainen et al., 1998), a prolonged exposure to high ambient N concentrations may threaten their vitality. *Sphagnum* mosses can acquire N in three ways: (1) from airborne drift via wet and dry deposition (e.g. Li and Vitt, 1997), (2) by recycling from older parts to the youngest, most actively growing ones (Aldous, 2002a; Malmer, 1988; Urban and Eisenreich, 1988), (3) by N_2 fixation (Damman, 1978; Hemond, 1983). During the first part of the experiment, under dry conditions, tracer input from the top was the main N source for the moss layer. Non-symbiotic N_2 fixation might have also played a role but was not assessed. Evidence for the significance of this process is limited to date. Waughman and Bellamy (1980) found bogs to generally have a low activity of nitrogenase and demonstrated an annual N_2 fixation of 0.07 $g\,N\,m^{-2}$, which is low in comparison to input by precipitation. However recently, Larmola and others (2013) estimated the annual N_2 fixation at the Finnish peatland to range from 0.1 to 2.9 $g\,N\,m^{-2}$ – values up to 10 times greater than the inorganic N deposition rate recorded at the studied region. As for the differing effect of raised water table on ^{15}N uptake by mosses and vascular plants we can only speculate. More N, particularly ammonium, from deeper, now inundated layers likely reached the living tissue of *Sphagnum* plants. This additional, ^{15}N-poor influx to the moss layer probably diluted the ^{15}N input from irrigation resulting in a lower *Sphagnum* ^{15}N content during the wet period (Fig. 3). Vascular plants, on the contrary, assimilated substantially larger amounts of the tracer during the second part of the experiment (Fig. 3). As the direct absorption of atmospheric N through leaf tissue is minimal, root uptake from pore water is the most common N supply for shrubs (Li and Vitt, 1997). Shrubs and some graminoids can experience problems when faced with continuously high water levels since they lack aerenchyma. It seems plausible that inundation led to a relocation of root activity to the upper, aerated peat layers, where more ^{15}N was present according to our measurements (Figs. 6 and 7) Murphy et al. (2009) suggested that shallow water tables in bog systems promote a shallower root distribution. It is also possible that more of the added ^{15}N surpassed the moss layer and entered the rooting zone of the vascular plants due to the generally raised N supply to the mosses when water table was high.

4.2 Nitrogen transformations and transport in the dissolved phase

The fact that the ^{15}N tracer penetrated deeper into the peat and more ^{15}N recovered from shrubs and graminoids in the cores from the sites with a legacy of strongly elevated N deposition (LV, FS) could, to some extent, confirm the hypothesis of increased N mobility and decreased retention in mosses and near-surface peat along the gradient of long-term N deposition (Table 1). We did not detect any N_2O fluxes but we observed

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dissolved inorganic N in the pore water and recorded higher concentrations of organic N at polluted sites. Concentrations of N_2O fluxes are difficult to quantify due to the episodic nature of N_2O production. Moreover, acidic conditions typical for ombrotrophic peatlands can slow down or even inhibit denitrification (Williams et al., 1999a). The increased concentrations of DIN and TDN detected below the *Sphagnum* layer might be an evidence of reduced retention of the *Sphagnum* layer caused by long-term elevated atmospheric N inputs at the study sites (FS). Such observation was, for example, made in the studies by Lamers et al. (2000) and Limpens et al. (2003). The concentrations of DON also increased along the background N deposition gradient (Table 1) and were highest at the Frölichshaier Sattelmoor site (Fig. 5). A similar pattern was recorded by Bragazza and Limpens (2004) during a field study of six European bogs spanning a range of chronic atmospheric N inputs from 0.2 to 2.0 $\mathrm{g\,m^{-2}\,yr^{-1}}$. In their study, both DIN and DON concentrations, measured in water samples collected from plots characterised by similar moss composition, increased with background N deposition but the latter increased more sharply. Baxter et al. (1992) reported an accumulation of amino acids in mosses receiving NH_4NO_3, which could be a potential source of DON released into the water surrounding mosses.

The tracer application as $NH_4{}^{15}NO_3$ indicates that all ^{15}N-ammonium found in pore water (Figs. 7 and 8) had to result from transformation of nitrate to ammonium. Such a process can either take place in the soil by microbial reduction (Hemond, 1983) or in the plant tissue by an enzymatic reduction of assimilated nitrate (Guerrero et al., 1981). At Degerö Stormyr, where only very little nitrate was present (Fig. 5), there was no potential for nitrate reduction. In Cors Fochno and Whixall Moss cores the ^{15}N application increased the amount of nitrate over the duration of the dry period (Fig. 5) and more $^{15}N\text{-}NH_4^+$ was found at these sites as well (Fig. 7). The highest $^{15}N\text{-}NH_4^+$ excess was recorded at Lille Vildmose, where also nitrate concentrations were high. In Frölichshaier Sattelmoor cores, where nitrate concentrations reached 38 $\mathrm{mg\,L^{-1}}$, most probably nitrate ammonification took place since ammonium accumulated towards the end of the dry period (Fig. 5). The lower isotopic signal recorded at the Frölichshaier Sattelmoor

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mesocosms could imply a dilution effect caused by lower concentration of N in the applied solution in comparison to the background N values.

The mechanisms of ammonium release may have changed along the N deposition gradient as suggested by the distribution of the ^{15}N tracer (Fig. 8) in the mesocosms: (1) at the sites with low N inputs (DS), nitrate was first assimilated by the plant layer and later apparently partly released as ammonium from the vascular plant roots, (2) at the sites with elevated N inputs (FS), some nitrate bypassed the living moss layer and was converted to ammonium in the pore water. However, this pattern does not necessarily indicate a loss of the *Sphagnum* filter. Even though the N content of *Sphagnum* tissue at Frölichshaier Sattelmoor was at $10 \pm 3.8\,\mathrm{mg\,g^{-1}}$ (Fig. 1) – the range encompassing the threshold N concentration suggested by Lamers et al. (2000) to inhibit further N content increase – the mosses did not suffer a substantial decline in biomass in the field and grew most of all in the experiment (Supplement, Table S1).

From our findings and earlier studies one may infer that N concentration is more important than N deposition rate for the moss filter function and the fate of N. A negative impact of high fertilizer concentration on moss growth was reported before (Pearce and Van der Wal, 2008; Pitcairn et al., 2006). Pearce and Van der Wal (2008) found that not the dose of N-containing solution but rather a high N concentration in irrigate impeded the growth of the moss *Racomitrium lanuginosum*. In the study analysing moss tissue N content in several transects across the UK, Pitcairn and others (2006) concluded that at sites dominated by wet deposition the rainfall NO_3^- and NH_4^+ concentration have more influence on moss tissue N than the total N deposition. Such a view has also been supported by recent ecosystem modelling. Wu and Blodau (2015) examined if low but frequent doses of N deposition differed in their impact on the distribution of shrubs, peat mosses, and grasses in a model simulation of the long-term N fertilization experiment at the Mer Bleue peatland (Ontario, Canada). In the fertilization experiment *Sphagnum* mosses had become nearly extinct after several years with seven applications of the N fertilizer per year, each being applied with 2 mm of irrigate (Juutinen et al., 2010). In the model a similar effect occurred when this fertilization scheme was adopted; daily

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application, however, entailed only an initial decline and subsequently a recovery of moss biomass at deposition levels of 3.2 to 6.4 g N m^{-2} yr^{-1} within 10 years of fertilization. Smaller rates of deposition at 1.6 g N m^{-2} yr^{-1} lead to increased moss biomass in the model simulations.

5 Conclusions

Our results confirm that a legacy of elevated N deposition in ombrotrophic peatlands, especially above levels of about 1.0–1.5 g N m^{-2} yr^{-1}, leads to lower retention of N, increased inorganic N concentrations in pore waters, and enhanced transfer of the deposited N to shrubs. Higher inorganic and organic dissolved N concentrations and more N in near-surface peat were found, and more of the ^{15}N label was recovered from the aboveground shrub biomass at the polluted sites compared to the nearly pristine Degerö Stormyr mire in Northern Sweden. As a consequence, a higher mobility of dissolved N in peat is probable under more realistic hydrologic conditions than present in our experiment. The shift to higher N mobility in the plant-peat soil system was, however, more gradual and modest than we expected. It was not visibly linked to the disappearance of *Sphagnum* mosses at the high long-term N deposition or to shifts in species composition, if the somewhat limited information from our most polluted site at the beginning of the 20th century is believed. Raised uptake of N by vascular plants along the N deposition gradient was accompanied by *Sphagnum* N absorption that was still high at the polluted sites. Some former studies (Bubier et al., 2007; Gunnarsson and Rydin, 2000; Juutinen et al., 2010) alluded that the vitality of *Sphagnum* suffers with increasing N saturation, which was undoubtedly the case in the mentioned fertilization studies. Under field conditions and our short-term experiments, however, concentrations of ammonium and nitrate in rain water remain lower and the filter function of mosses appears to remain mostly intact, even at deposition levels considerably higher than 1.0–1.5 g N m^{-2} yr^{-1}.

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Table 1. Characteristics of the sampled peatlands. Site specific data – DS (Granberg et al., 2001; Sagerfors, 2007), CF, WM http://www.metoffice.gov.uk/climate/uk/averages/19712000/, LV (Charman and Blundell, 2007), FS (Baumann, 2009; Jensen, 1990). N and S deposition data (wet and dry deposition) – national models: DS (Karlsson et al., 2012), CF and WM for year 2009 – Department for Environment Food and Rural Affairs (DEFRA) accessed August 2012 at http://pollutantdeposition.defra.gov.uk/data, LV for year 2004 (Ellermann et al., 2004), FS for 1993 (Gauger, 2009), – measured values: DS for 1990–1992 (Granberg et al., 2001), CF and WM data not available, LV (Ellermann et al., 2004), FS (Böhlmann et al., 2005), – IDEM model (Pieterse et al., 2007). [*] The area of Fenn's, Whixall and Bettisfield Mosses Abbreviations: Lat – latitude, Long – longitude, MAP – mean annual precipitation, MAT – mean annual temperature, MASL – meters above sea level, bsl – below sea level, IDEM – Integrated Deposition Model (Bleeker et al., 2004).

Sites	Degerö Stormyr (DS)	Cors Fochno (CF)	Whixall Moss (WM)	Lille Vildmose (LV)	Frölichshaier Sattelmoor (FS)
Country	Sweden	Wales	England/Wales	Denmark	Germany
Lat (N)	64.181	52.502	52.915	56.846	51.791
Ling (E)	19.559	−4.011	−2.771	10.183	10.531
MAP (mm)	602	1035	747	633	1222
MAT (°C)	1	9.7	8.7	7.6	5.2
MASL	277	4	91	8	765
Area (km^2)	6.5	10	9.48[*]	20	0.18
Type	bor. mire	raised bog	raised bog	raised bog	raised bog
pH[*]	3.73 ± 0.11	4.11 ± 0.19	3.70 ± 0.25	3.95 ± 0.12	3.89 ± 0.20
N deposition national models ($g\,N\,m^{-2}\,yr^{-1}$)	< 0.2	0.8	1.2	1.6	5.5–6.0
N deposition measured ($g\,N\,m^{-2}\,yr^{-1}$)	0.2	n.a.	n.a.	1.7	4.7
N deposition IDEM ($g\,N\,m^{-2}\,yr^{-1}$)	0.21	0.36	1.05	1.37	1.43
S deposition national models ($g\,S\,m^{-2}\,yr^{-1}$)	0.3	0.21	0.23	0.65	5.5–6.0
Mean peat depth (m)	5	7	8	4–5	2.5–3.5
Water table level low/high (cm bsl)	17/7.5	15/0.5	23/2	31/1	30/2
Vegetation					
Sph. capilifolium[*]		×	×		
Sph. fallax[*]			×		
Sph. magellanicum[*]				×	
Sph. papillosum[*]					×
Sph. pulchrum[*]		×			
Sph. rubellum[*]	×				
Andromeda polifolia[*]	×	×	×	×	×
Calluna vulgaris		×	×	×	×
Erica tetralix[*]		×	×	×	
Rubus chamaemorus	×				
Vaccinium oxycoccos	×		×	×	×
Eriophorum vaginatum[*]	×	×	×	×	×
Eriophorum angustifolium[*]		×	×	×	

Table 2. Recovery of ^{15}N (%) for all sites and percent contribution of N ecosystem pools to the total recovery at each site after 24 weeks of tracer application. Standard deviations are given in parenthesis.

Site	NO_3^-	NH_4^+	*Sphagnum* (0–5 cm)	Shrubs	Graminoids	Peat	Total recovery
Degerö	0.011	0.003	65.6	3.8	1.8	59.8	**131.0**
Stormyr	(0.002)	(0.003)	(22.6)	(1.0)	(0.5)	(45.8)	(25.3)
Cors	0.043	0.163	40.4	6.2	0.8	57.0	**104.7**
Fochno	(0.045)	(0.030)	(15.0)	(3.4)	(0.3)	(18.7)	(12.0)
Whixall	0.014	0.284	23.6	5.4	0.4	68.9	**98.7**
Moss	(0.002)	(0.134)	(9.5)	(3.3)	(0.4)	(7.2)	(6.3)
Lille	0.031	0.661	57.8	5.7	1.4	21.9	**87.5**
Vildmose	(0.025)	(0.282)	(23.7)	(5.1)	(1.2)	(20.9)	(16.2)
Frölichshaier	0.051	0.374	45.5	12.4	1.2	36.2	**95.7**
Sattelmoor	(0.037)	(0.065)	(6.3)	(4.3)	(1.6)	(12.8)	(6.5)

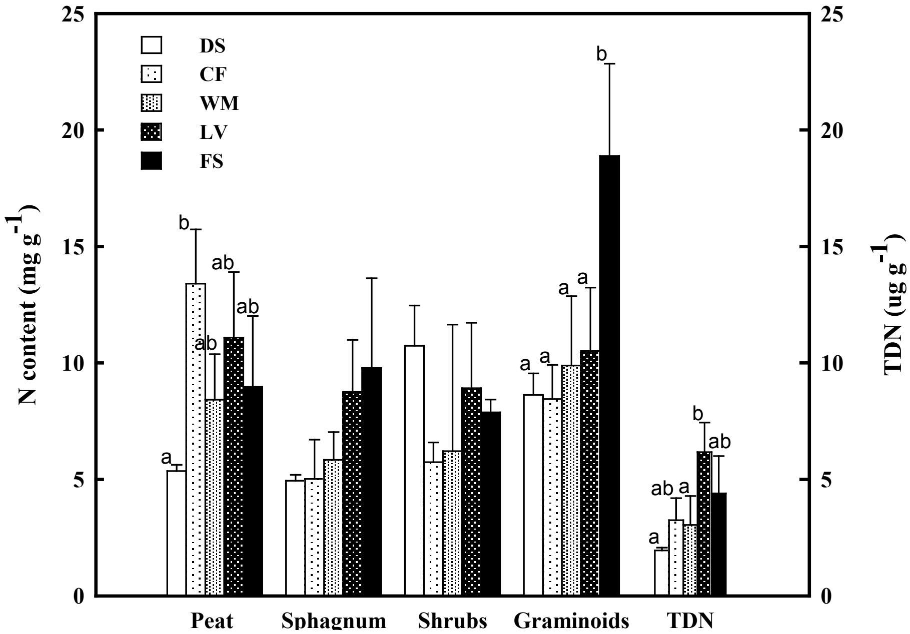

Figure 1. Nitrogen content (mean ± SD, $n = 3$) of peat (5–15 cm depth), *Sphagnum* (0–5 cm below surface), shrub, graminoid and total dissolved nitrogen (TDN) (0–15 cm depth) pools. Letters *a* and *b* – significant differences in the mean values of the sites at each pool (One Way ANOVA, Tukey Test). A bar without a letter – no significant difference. Site abbreviations: DS – Degerö Stormyr, CF – Cors Fochno, WM – Whixall Moss, LV – Lille Vildmose, FS – Frölichshaier Sattelmoor.

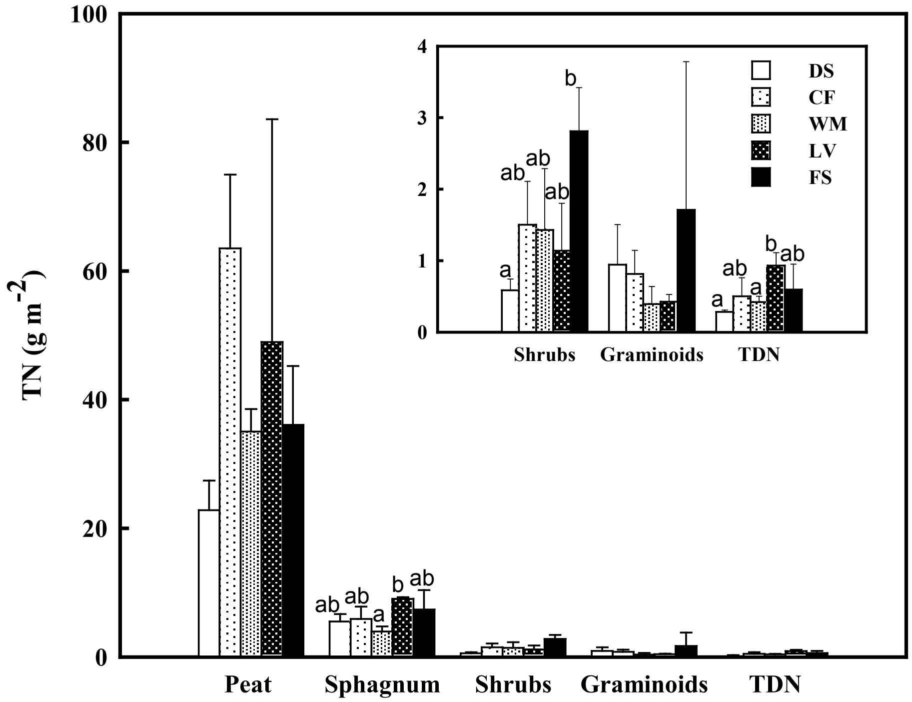

Figure 2. Total nitrogen content (mean ± SD, $n = 3$) in the ecosystem pools investigated. The *Sphagnum* pool contained mass from 0 to 5 cm below surface. Letters *a* and *b* – significant differences in the mean values of the sites at each pool (One Way ANOVA, Tukey Test). A bar without a letter – no significant difference. Site abbreviations as in Fig. 1.

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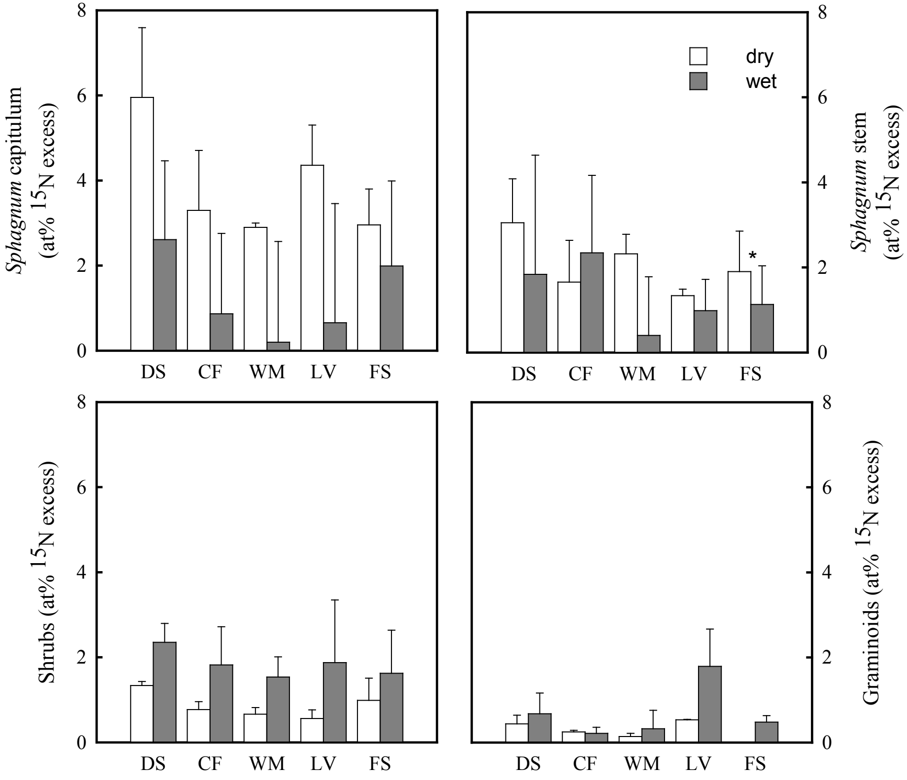

Figure 3. ^{15}N abundance (mean ± SD, $n = 3$) expressed as at% ^{15}N excess in vegetation during dry (dry) and during wet (wet) period. **(a)** *Sphagnum* capitulum, **(b)** *Sphagnum* stem, **(c)** shrubs, **(d)** graminoids. One Way ANOVA indicated a significant effect of dry and wet period for *Sphagnum* capitulum and shrubs, a Tukey post-hoc test failed to identify significant differences for individual treatments, however. Significant differences using a pairwise t test between dry and wet period at individual sites are marked with an asterisk (*). Site abbreviations as in Fig. 1.

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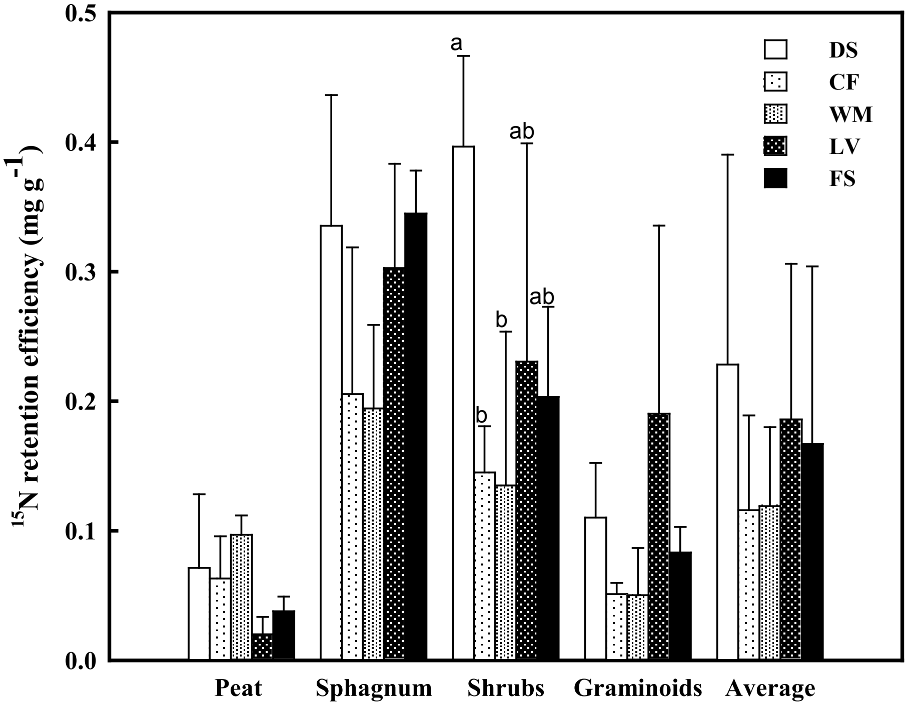

Figure 4. ^{15}N retention efficiency (mean ± SD, $n = 3$) of ecosystem pools, calculated by dividing retained ^{15}N in each pool by mass of the corresponding pool. "Average" represents the mean ^{15}N retention efficiency of all pools (mean ± SD, $n = 4$). Letters *a* and *b* – significant differences in the mean values of the sites at each pool (One Way ANOVA, Tukey Test). A bar without a letter – no significant difference. Site abbreviations as in Fig. 1.

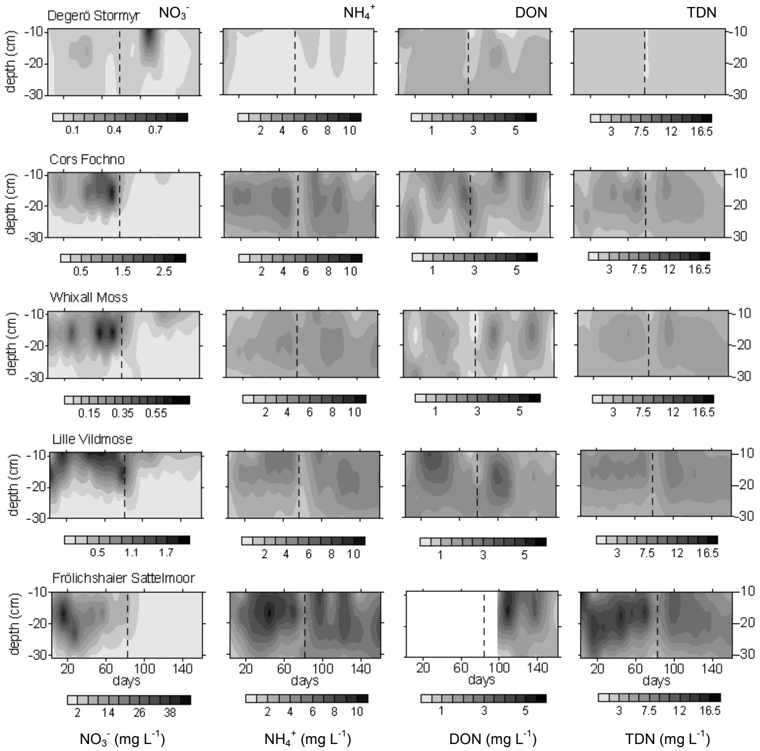

Figure 5. Dissolved nitrogen concentrations in the pore water: nitrate (NO_3^-), ammonium (NH_4^+), dissolved organic nitrogen (DON) and total dissolved nitrogen (TDN) Please note the varying scale bars for NO_3^-. Vertical dashed line marks the transition between dry (left) and wet (right) period.

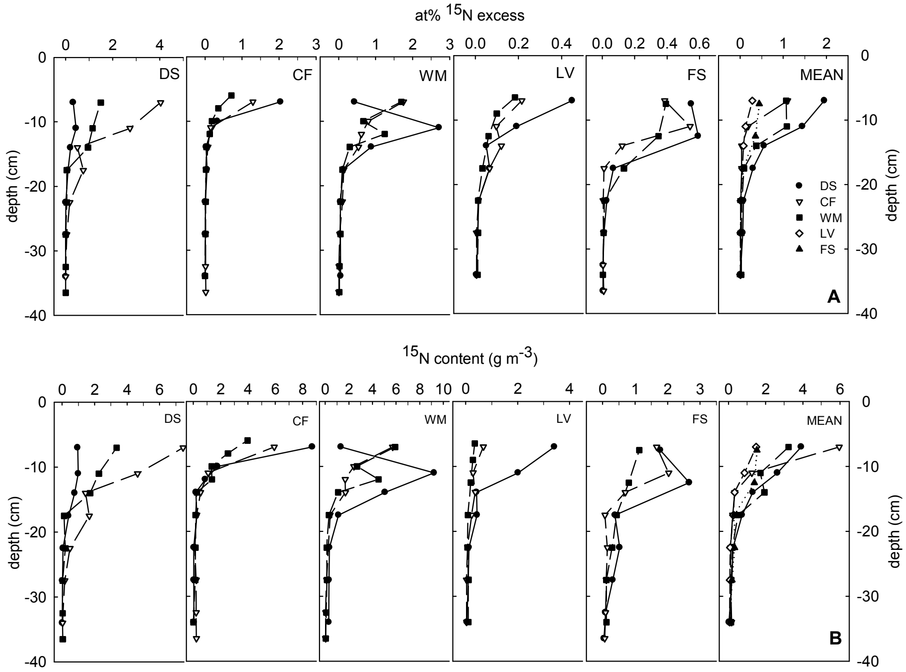

Figure 6. Depth profiles of peat at% ^{15}N excess **(a)** and peat ^{15}N content **(b)** for three replicate cores from each site (6–9 samples core^{-1}) and the mean at% ^{15}N excess and peat ^{15}N content for each site. Site abbreviations as in Fig. 1.

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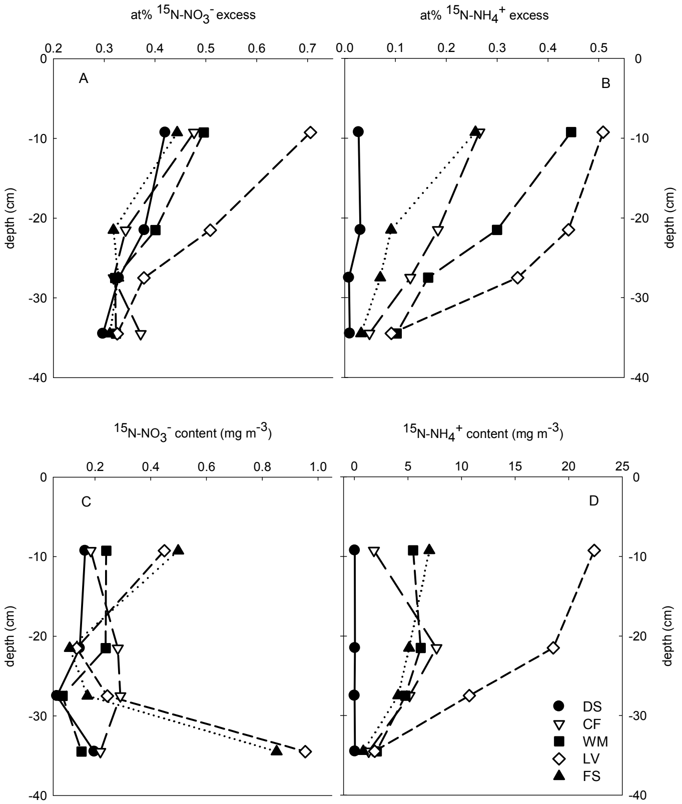

Figure 7. Pore water ^{15}N excess and ^{15}N content: **(a)** ^{15}N-nitrate (at% excess), **(b)** ^{15}N-ammonium (at% excess), **(c)** ^{15}N-nitrate (mg m^{-3}), **(d)** ^{15}N-ammonium (mg m^{-3}).

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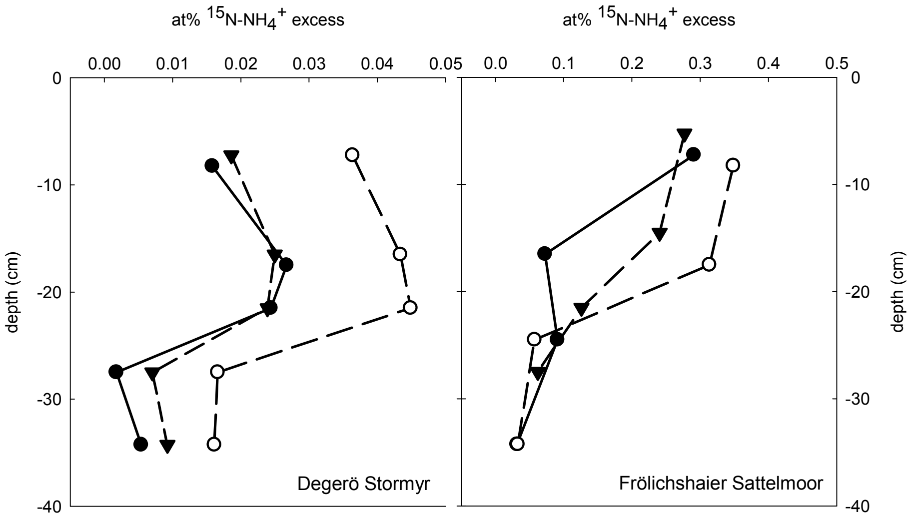

Figure 8. Atom% ^{15}N-NH$_4^+$ excess in pore water of three replicates from Degerö Stormyr (left) and Frölichshaier Sattelmoor (right). Each symbol in the profile represents the middle depth of the section from which the water was extracted.