Water, soil and vegetation under the influence of high atmospheric nitrogen deposition in a cutover and rewetted raised bog in Northwest Germany

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SUMMARY

Bogs located near agricultural areas often receive high atmospheric nitrogen (N) depositions, and this may result in an increased soil and water N pool and enhanced N supply for plants and microorganisms. The consequences are changes in plant species composition and diffuse emissions of N species from these bogs. However, research on the resilience of rewetted bogs to high atmospheric N inputs is still sparse. Our aim was to evaluate the influence of N depositions on a bog that was rewetted after peat extraction down to bare 'black' (highly decomposed) bog peat. We monitored dry (NH_3) and wet (NH_4^+ and NO_3^-) deposition, and plant available N as NH_4^+ and NO_3^- in soil and water, over the course of one year. The amount of N stored in vegetation was also quantified. We detected a total N deposition of 32 kg ha^{-1} y^{-1} which by far exceeded the critical load (5–10 kg ha^{-1} y^{-1}) for bogs, but there were no signs of deposition induced N increase in soil and bog water. Our findings suggest, rather, that levels of plant available N were crucially affected by mineralisation in areas with lower water table. Depending on the sampling station, the amount of N stored in the vegetation was 23 or 30 kg ha^{-1}. Although it was likely that uptake by vegetation played a decisive role in buffering the high N depositions, it did not completely explain the whereabouts of excess N. Accordingly, other processes like peat growth, N removal by mowing or denitrification must have contributed to buffering N levels in soil and water.

KEY WORDS: Leegmoor, mineralisation, nitrogen content, nitrogen load, nutrient relocation, restoration

INTRODUCTION

Because bogs are solely rainfed their only nutrient source is atmospheric input, via wet deposition with rain or dry deposition of particles (Sjörs 1980). This, in combination with the continuously waterlogged conditions hampering biochemical mineralisation, makes them naturally nutrient poor ecosystems that are easily disturbed by excessive availability of nutrients (Urban & Eisenreich 1988, Bourbonniere 2009). In this context a crucial element is nitrogen (N), which is usually the growth limiting element in bogs under natural conditions and can become abundant either through mineralisation under aerobic conditions (Bridgham *et al.* 1998, Venterink *et al.* 2002) or through increased atmospheric N depositions (Aerts *et al.* 1992).

Holland *et al.* (1999) estimated that the average N deposition on non-forested wetlands in the temperate northern hemisphere was 0.59 kg ha^{-1} y^{-1} in pre-industrial times. However, both the magnitude and the spatial distribution of global N depositions have shifted substantially during recent decades. Several studies have shown that intensive agriculture is the most important driver for the increase of atmospheric N depositions. Fangmeier *et al.* (1994) showed that about 90 % of ammonia (NH_3) emissions came from livestock and fertilisers, and this promoted the transition of heathland into grassland (to a large extent *Molinia caerulea*).

The N uptake capacity of natural bog vegetation is mainly associated with uptake by peat moss (*Sphagnum*) species. Fritz *et al.* (2014) showed that the N uptake capacity of *Sphagnum magellanicum* decreased rapidly under increased N depositions and that N loads exceeding the uptake capacity of the *Sphagnum* led to higher N availability for root uptake by vascular plants, promoting competition and species conversion. An experiment by Tomassen *et al.* (2003) revealed that *Molinia caerulea* responded rapidly to an increased N supply, and additional N still stimulated the growth and dispersion of this plant species after three years, even under phosphorous (P) limitation. Regarding the turning point from low N concentration in the soil or water to higher N levels, literature data differs between N depositions of 32 kg ha^{-1} y^{-1} (van den Elzen *et al.* 2018) and 64 kg ha^{-1} y^{-1} (Sheppard *et al.* 2013, Chiwa *et al.* 2016).

The threshold for N tolerance of a specific ecosystem is described by the critical load (CL). Exceedance of the empirical CL value increases the probability of change in the ecosystem. The range of CLs for raised bogs is 5–10 kg ha^{-1} y^{-1} and exceedance leads to increased abundance of vascular plants, elevated N contents or concentrations in soil and water, and changes in bryophyte species composition.

Large areas in the state of Lower Saxony in Northwest Germany are intensively managed for agriculture (MU 2016). For a semi-natural bog in this region, Mohr *et al.* (2013) and Hurkuck *et al.* (2014) showed that NH_3-N arising from manure and fertiliser from the surroundings accounted for more than 80 % of the dry deposited N. *Molinia caerulea* meadows are nowadays amongst the predominant degraded bog types in Northwest Germany (MU 2016). For these degraded bog ecosystems the CL is 15–25 kg ha^{-1} y^{-1} and exceedance increases the abundance of graminoids at the expense of bryophytes, reducing general diversity (Bobbink *et al.* 2015). However, research on the resilience of rewetted bogs in this region to high atmospheric N inputs is still sparse.

The study described in this article aimed to improve our understanding of how resilient rewetted bogs are towards high atmospheric N depositions. It was conducted on the industrially cutover bog known as the "Leegmoor" in Lower Saxony, which was rewetted in the 1980s. The Leegmoor is surrounded by agricultural land and a previous (1984–1988) study estimated that the atmospheric N input by wet deposition (only) was 27.1 kg ha^{-1} y^{-1} (Nick *et al.* 1993). More recently we demonstrated that concentrations of NH_4^+ and NO_3^- in soil and water of the Leegmoor had either remained nearly constant or decreased slightly since that time (Nachtigall & Giani 2022). On this basis we hypothesised that: (1) the Leegmoor must still receive atmospheric N depositions from adjacent agricultural areas that considerably exceed the CL of 5–10 kg ha^{-1} for bog ecosystems; (2) given the N levels observed in soil and water, a significant proportion of the N depositions must be stored in the vegetation that has newly developed since rewetting; and (3) levels of plant available N in soil and water of a sampling station with lower water table should exceed those at a location with higher water table due to enhanced peat mineralisation. The objective of this study was to compare the role of atmospheric N depositions and peat mineralisation in providing plant available N species in soil and water, between two locations with different water table conditions. Accordingly, the study reported here was guided by the following questions:

(1) How high are atmospheric N depositions at the Leegmoor?

(2) How much N is stored in the vegetation?

(3) How much N is added to the plant available soil and water N pool by peat mineralisation?

(4) What are the comparative roles of atmospheric N depositions and peat mineralisation in providing plant available N species in soil and water, between two locations with different water table conditions?

METHODS

Study site

The Leegmoor (52° 59′ 34″ N, 7° 33′ 20″ E) is a raised bog situated within the intensively managed agricultural area of Lower Saxony in Northwest Germany. The superficial layer of less-decomposed ('white') peat was industrially extracted during the 20th century, leaving more strongly decomposed 'black' peat at the surface. Both white and black peat are characterised as bog peat and developed solely under rainwater influence, although their different humification degrees originated from different climatic conditions during the history of peat formation (NLWKN 2022). In other words, black peat is distinct from fen peat, in that it is practically sealed off from underlying soil layers preventing groundwater contact. In cutover peatlands, the near-surface black peat layers may be influenced by groundwater in some parts, owing to the low thickness of the remaining peat layer. However, this can be ruled out in the Leegmoor because the hydrochemistry is bog typical (see Results and Discussion sections).

The bog was rewetted in the 1980s (for a detailed description, see Nachtigall & Giani 2022). Its vegetation is nowadays a mosaic of mainly *Sphagnum cuspidatum*, *Molinia caerulea*, *Betula pubescens*, *Eriophorum* species, *Calluna vulgaris* and *Erica tetralix*. The findings presented in this article were obtained in the framework of a joint study (see Blankenburg *et al.* 2023) with the objective of monitoring the success of the Leegmoor restoration. Additional instrumentation that is relevant to this article include a weather station for climatic observations (logged April 2019 to December 2021) and two of the nine bog wells for monitoring of bog water levels (logged January 2019 to December 2021). The locations of these instruments are indicated in Figure 1, and the data they provided are shown for the measuring period February 2020 to February 2021 only.

Field sampling

Field sampling was conducted between February 2020 and February 2021. The amount of precipitation and the temperature at 1 m above ground level were measured at the established weather station (Figure 1) (Blankenburg *et al.* 2023). All other sampling was conducted at the two sampling stations P1highWT and P2lowWT (Figure 1), which were selected according to the following two criteria. First, they should be located at a reasonable distance from one another so that any spatial heterogeneity of dry N deposition across the study site would be discernible. Secondly, they should have different water table levels. The water table was higher at P1highWT in the north than at P2lowWT in the south (see the subsection "soil properties" in the Results section for details). The difference in water table between P1highWT and P2lowWT was determined by comparing the bog well data (Blankenburg *et al.* 2023).

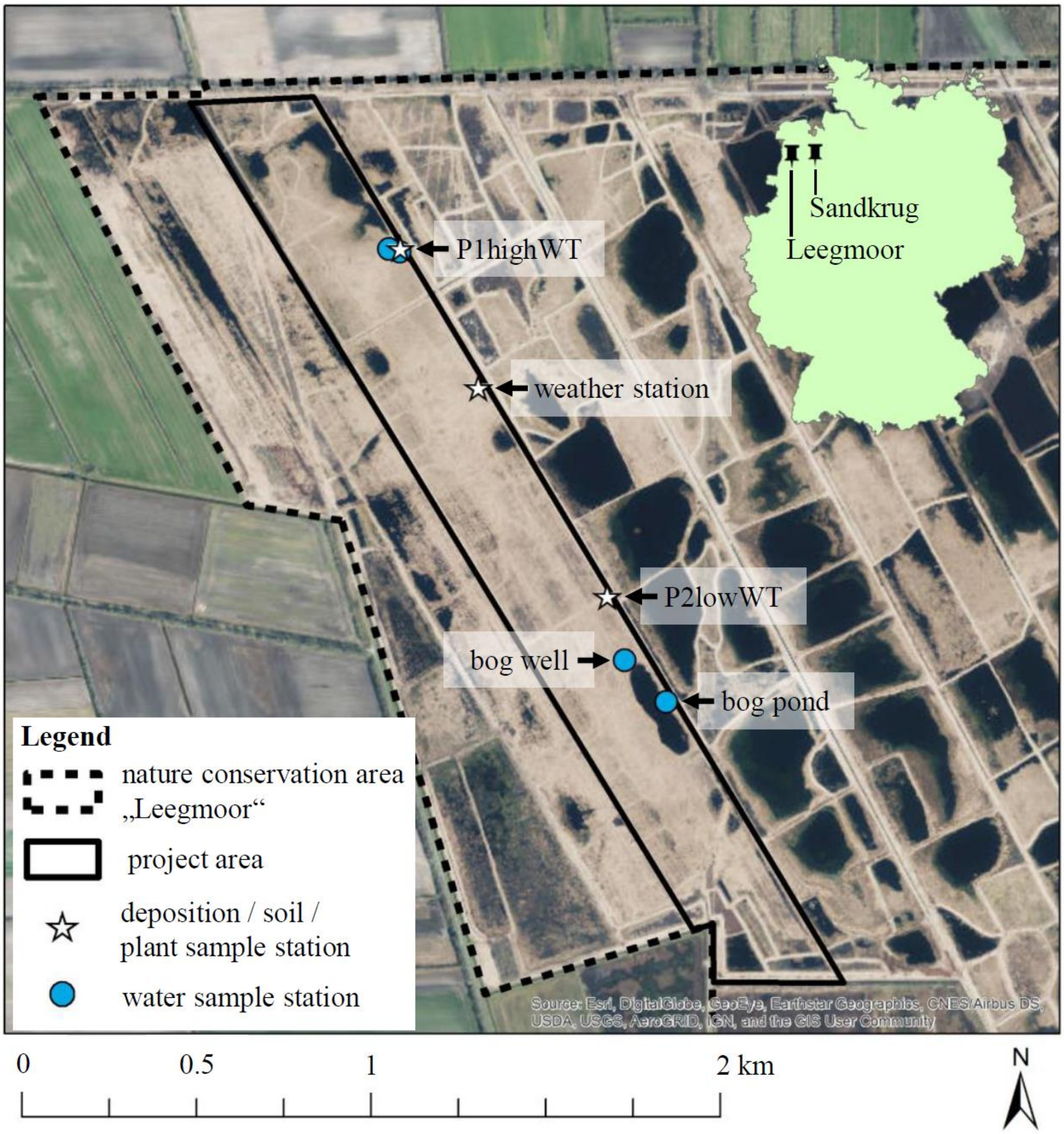

Figure 1. Map of the "Leegmoor" project area in Northwest Germany. P1highWT: sampling station in the north with higher water table; P2lowWT: sampling station in the south with lower water table; bog and surface water sampling stations at P1highWT are located directly at the passive sampling station; water sampling stations at P2lowWT are indicated as bog well (bog water sampling) and bog pond (surface water sampling).

Atmospheric N depositions

We used passive samplers (type IVL, as described by Dämmgen *et al.* 2010) to determine dry depositions by means of NH_3 concentration in the ambient air. Each sampler was equipped with a sorption filter (cellulose, 0.45 µm, impregnated with a solution of phosphoric acid) and a turbulence inhibitor (Polytetrafluoroethylene membrane, 1 µm). At each of the two sampling stations, four samplers were deployed about 2 m above ground level, in a device protecting them from bird droppings mounted on measuring poles, in February 2020. Thereafter, the samplers were collected and replaced at monthly intervals until February 2021. Each month the samplers were removed from the device and wiped with a paper towel before placing them in a closable polyethylene (PE) tube for transportation. For each sampling set a fifth sampler was deployed in its tube to provide a field blank value. Before deployment and after collection (until further treatment), the tubes containing prepared samplers were normally stored in a desiccator. However, a temporary closure of the laboratory due to Covid-19 restrictions meant that the samplers deployed in May and June 2020 could not be stored in this way.

For wet depositions we used bulk samplers (as described by Mohr *et al.* 2005) to collect precipitation samples. Precipitation samples were collected every two weeks and the merged samples of four weeks were subsequently analysed. Unfortunately, the temporary laboratory closure limited capacities for both storage and analysis of samples. Because dry depositions are the most decisive fraction for the total deposition (as outlined above under ‘Introduction’), the measurements of N fluxes in the Leegmoor were reduced to dry depositions only and the measurements of wet deposition were discontinued from March 2020. Instead, wet deposition data from the research site “Sandkrug” (53° 1′ 17″ N, 8° 16′ 58″ E, distance from the Leegmoor about 50 km; see Figure 1) were used. These data were collected within a long-term N deposition monitoring programme conducted by the Lower Saxony Chamber of Agriculture (co-author K. Mohr). The Sandkrug sampling site is located in an open land area. The substitution of data from Sandkrug is justified on the basis that the levels of wet N deposition and oxidised N species (NO_x) in the rural lowlands of Northwest Germany are known to vary by only 5–10 %, mainly owing to weather and measurement tolerance (Mohr *et al.* 2005, UBA 2022). Wet N depositions were calculated by multiplying NH_4^+ and NO_3^- concentrations by the amount of precipitation.

Soil, water and plants

Bulk soil samples were collected monthly, on the same dates as the passive N samplers, using a sampling spoon that has a conical shape to prevent core loss when sampling waterlogged soils (custom-built by the Institute’s mechanics workshop). A set of three cores was split into two sampling depths, 0–15 cm and 15–30 cm respectively, and thereafter combined into one mixed sample per depth and site. The samples were placed in PE bags, stored in a dark and cool box for transportation, and refrigerated at 4 °C in the laboratory until further treatment.

Undisturbed soil samples for bulk density were collected once in summer 2020, using 100 cm^3 steel rings. At P2lowWT, samples were extracted from depths of 5–10 cm and 20–25 cm with three replicas for each depth. At P1highWT the soil below 10 cm depth was too wet to collect undisturbed samples, so the bulk density determined for the 5–10 cm layer was assumed also to represent the 20–25 cm layer. The steel rings containing soil samples were closed with lids at each side, stored in a box for transportation, and refrigerated at 4 °C in the laboratory until further treatment.

Surface and bog water were collected monthly, again on the same sampling dates as for dry deposition. Surface water samples were obtained from intermittent standing water at the sampling station P1highWT and from a bog pool (Figure 1) near P2lowWT, where there was never standing water on the bog surface. Bog water samples were obtained from the nearby bog wells using a submersible pump (Eijkelkamp “Gigant”). The samples were collected in PE bottles (250 mL), stored in a dark box for transportation, and refrigerated at 4 °C in the laboratory until further treatment.

Plant samples were collected on one occasion in July 2020. Plant species cover was estimated according to Braun-Blanquet (1964) in a 10 × 10 m square centred on the sampling station. Root samples were obtained from a whole *Molinia caerulea* plant at P1highWT only, as no whole *Molinia caerulea* plant could be obtained from P2lowWT. Roots of other plant species were ignored because their biomass was negligible compared to the deep and massive roots of *Molinia caerulea*. Shoot samples of *Molinia caerulea*, *Eriophorum vaginatum*, *Betula pubescens*, *Calluna vulgaris* and *Erica tetralix* were collected at the two sampling stations by harvesting five whole shoots of each. *Sphagnum* samples were obtained at both sampling stations by harvesting ten patches of 10 × 10 cm. The samples were placed in PE bags for transportation.

Laboratory analyses

Atmospheric N depositions

The concentration of NH_3 (µg m^{-3}) in the ambient air was determined by means of photometric analysis according to VDI 3869 (2010). Concentrations of NH_3, accumulated as NH_4^+, in the extracted filter eluates from the IVL passive samplers were measured photometrically according to DIN 38406-5 in a Shimadzu UVmin-1240. The results for May and June 2020 were implausible, presumably owing to improper storage of the samplers, and were not considered further.

The NH_4^+ and NO_3^- concentrations (mg L^{-1}) in precipitation from the bulk samplers for wet deposition were determined by flow analysis and photometric detection according to DIN EN ISO 11732:2005-05 and DIN EN ISO 13395:1996-12 with preceding filtration at a mesh size of 0.45µm.

Soil, water and plants

NH_4^+ and NO_3^- (later referred to as plant available NH_4^+ and NO_3^-) concentrations in soil (mg kg^{-1}) and water (mg L^{-1}) samples were measured according to VDLUFA (1997) and Blume *et al.* (2011). Water samples were filtered (mesh 8–12 µm, which is the standard mesh for this method). Soil samples were extracted by shaking 25 g of fresh soil with 100 mL of 0.0125 M $CaCl_2$ for 30 min, with subsequent filtration (mesh 8–12 µm). NH_4^+ and NO_3^- concentrations were measured by fractioned steam distillation in an Omnilab FoodALYT D 3000 and subsequent titration with 0.0025 M H_2SO_4 in a Schott Titronic 96.

Water pH was measured before filtration. Soil pH was measured according to Blume *et al.* (2011): 5 g of each composite fine soil sample was blended with 25 mL of 0.01 M $CaCl_2$ or distilled water and left for 60 min to equilibrate. pH was measured with a mobile pH meter (Knick Portamess 911 pH).

The total N (N_t) of plant and soil samples (g kg^{-1}, dry mass basis) was obtained by C/N elemental analysis (Thermo Fisher Scientific, Flash 2000). The various materials were prepared for this analysis as follows. Fine soil was produced from the disturbed soil samples by drying at 40 °C and passing through a 2 mm sieve. Plant samples were weighed fresh and washed with demineralised water. Then, to produce dry matter (DM), they were dried at 60 °C, weighed dry and then shredded. Samples of *Betula pubescens* were separated into wood and leaves beforehand. Composite samples for testing were then produced by combining equal amounts of shredded plant material and fine soil from the individual replicate samples, then blending and grinding to powder in a ball mill before weighing out duplicate samples (2–3 mg) into tin cups.

Bulk density (of the undisturbed soil samples) was measured according to DIN 19672-1, as the quotient of sample mass after drying at 105 °C and the calculated (cylinder) volume of the sampling ring.

Soil water content (wt.-%) was measured according to VDLUFA (1991). A fresh sample (5 g) of soil was dried at 105 °C and the difference between its fresh and dry weights was calculated.

Data analysis

Means and standard deviations were calculated in MS Excel (MS Office Version 365, 2022). The map was created using Esri ArcMap (Version 10.6). Statistical tests were performed in IBM SPSS (Version 28). Normal distribution was tested using the Kolmogorov-Smirnov test. NH_4^+ concentrations in surface and bog water and soil NH_4^+ contents did not follow normal distributions, so differences between the sampling stations were tested using the Wilcoxon-Mann-Whitney test. NH_3 concentrations of the ambient air and N_t contents of plant samples were normally distributed, so statistical differences between the sampling stations were determined by the independent t-test. Statistical correlations were calculated by Spearman's rank correlation coefficient. Plant available N contents in the soil (kg ha^{-1}) were calculated using our measurements of bulk density and soil water content.

The plant N pool was calculated as follows:

$$N_A = \frac{DM \times \frac{N_r}{100}}{A} \times 10 \times \frac{cover}{100} \qquad [1]$$

where N_A (kg ha^{-1}) is the amount of N_t per unit area of the respective plant species, *DM* is the plant dry matter (g), N_r (%) is the fraction of N in the dry matter, A (m^2) is the area covered by the individual plant sample, multiplying by 10 converts from g m^{-2} to kg ha^{-1} (×10,000/1,000), and *cover* (%) is the overall plant species cover at the sampling station. This calculation was repeated for the root samples and subsequently the N_t contents of all plant species were summed to obtain the total N_t pool per unit area at the respective sampling stations.

Wet deposition was calculated from the amount of precipitation measured at the Leegmoor weather station and the measured concentrations of NH_4^+ and NO_3^- in precipitation at Sandkrug (Figure 1). NH_3 deposition was determined from the concentration of NH_3 in ambient air using the inferential method according to VDI 3869 (2010):

$$\beta_0 = \frac{m_s \times l}{A_{Pr} \times D \times t} \quad [2]$$

where β_0 is the concentration of NH_3 in the ambient air ($\mu g\ m^{-3}$), m_s is the absolute amount of NH_3 on the exposed filter (µg), l is the length of the tube (1 cm), A_{Pr} is the area of the aperture (= 3.14 cm^2), D is the molecular diffusion coefficient of NH_3 (= 0.254 $cm^2\ s^{-1}$ at 25 °C; temperature correction was not performed because, in the range 275–312 K, the influence of temperature on the collection rate is negligible (< 0.1 %), see VDI 3869 (2010)), and t is the duration of measurement (s). The NH_3 deposition was calculated by multiplying β_0 by the velocity of deposition (= 0.01 m s^{-1}) and converting to units of kg NH_3-N ha^{-1} y^{-1} (Mohr *et al.* 2013). Micrometeorological measurements by Mohr *et al.* (2013) in the comparable bog "Bourtanger Moor", situated in a rural area with a low NO_x pollution level approximately 50 km from the Leegmoor, showed that NH_3-N makes up 80 % of total dry deposition. Therefore, to estimate total dry deposition at the Leegmoor, we added 20 % to the measured NH_3-N deposition to account for residual dry deposition (including HNO_3-N, HNO_2-N, particulate NH_4-N, particulate NO_3-N).

RESULTS

N deposition

The amount of precipitation ranged from 3 to 196 mm per month with a monthly mean of 65 ± 51 mm and an annual total of 843 mm, which exceeded the long-term average at the nearby climate station "Dörpen" (52° 57' 15" N, 7° 19' 10" E, distance from the Leegmoor about 16 km) by 39 mm (DWD 2022). Mean annual temperature at the Leegmoor was 10.1 °C and only slightly higher than the long-term average of 9.9 °C at Dörpen. Concentrations in precipitation of NO_3^--N ranged from 0.19 to 0.86 mg L^{-1} with a mean of 0.45 mg L^{-1}, and of NH_4^+-N from 0.24 to 2.08 mg L^{-1} with a mean of 0.87 mg L^{-1}. The concentrations of both NO_3^--N and NH_4^+-N peaked in April (Figure 2). Monthly wet deposition of NO_3^--N ranged from 0.02 to 0.88 kg ha^{-1} with a mean of 0.25 kg ha^{-1} and an annual total of 3.22 kg ha^{-1} (Figure 3). Monthly wet deposition of NH_4^+-N ranged from 0.05 to 1.84 kg ha^{-1} with a mean of 0.45 kg ha^{-1} and an annual total of 5.90 kg ha^{-1}.

NH_3-N concentrations in the ambient air at P1highWT ranged from 2.55 to 20.7 $\mu g\ m^{-3}$ with a mean of 8.01 $\mu g\ m^{-3}$, and at P2lowWT they ranged from 4.08 to 17.6 $\mu g\ m^{-3}$ with a mean of 7.86 $\mu g\ m^{-3}$, peaking in April at both sampling stations (Figure 4).

The calculated dry NH_3-N deposition at P1highWT ranged from 0.45 to 4.57 kg ha^{-1} per month with a monthly mean of 1.85 kg ha^{-1} and an annual total of 18.5 kg ha^{-1}, whereas at P2lowWT it ranged from 0.73 to 3.88 kg ha^{-1} per month with a monthly mean of 1.79 kg ha^{-1} and an annual total of 17.9 kg ha^{-1}. The mean dry NH_3-N deposition at both locations was 18.2 kg ha^{-1} y^{-1} (Figure 3). Differences between P1highWT and P2lowWT were negligible and not statistically significant ($p > 0.05$).

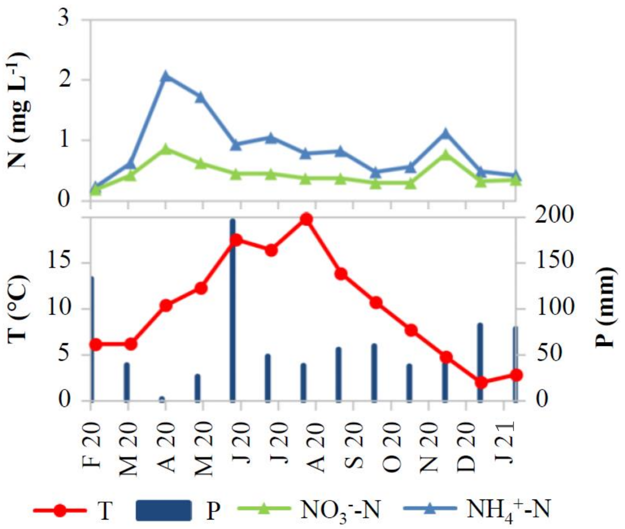

Figure 2. Precipitation (P), mean temperature (T) and concentrations of NH_4^+-N and NO_3^--N in precipitation samples over the course of the year.

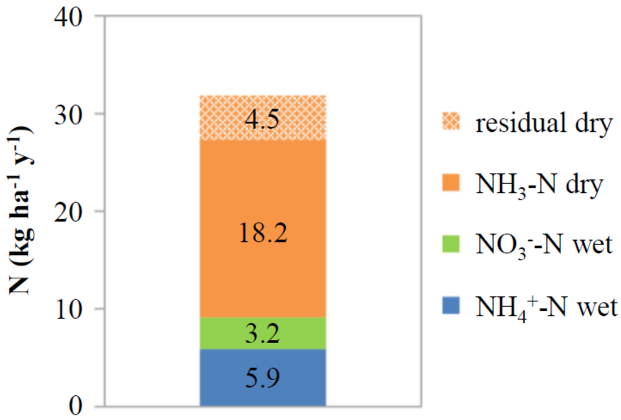

Figure 3. Total annual N deposition calculated as averages of monthly measurements between February 2020 and February 2021. 'Residual dry' is a literature-based estimate that includes HNO_3-N, HNO_2-N, particulate NH_4-N and particulate NO_3-N deposition.

The estimated total N deposition amounted to 31.9 kg ha^{-1} y^{-1}, consisting of 5.9 kg NH_4^+-N ha^{-1} y^{-1}, 3.2 kg NO_3^--N ha^{-1} y^{-1}, 18.2 kg NH_3-N ha^{-1} y^{-1} and 4.5 kg residual dry N ha^{-1} y^{-1} (Figure 3). None of the deposition fractions (wet NH_4^+-N, wet NO_3^--N, dry NH_3-N) was correlated with NH_4^+-N concentration in the surface or bog water, or with soil NH_4^+-N content ($p > 0.05$).

Soil properties

During the measuring period the water table at P1highWT fluctuated between 6 cm above and 24 cm below ground level, with an average position of 6 cm below ground level. Water table levels at P2lowWT ranged from 5 cm above to 55 cm below ground level with an average of 17 cm below ground level.

The pH ($CaCl_2$) at both locations was 2.8 for all sampling depths, pH (H_2O) was 3.3 in all samples except P2lowWT (15–30 cm), where it was 3.1. Bulk density at P1highWT was 0.11 g cm^{-3} in the 0–15 cm layer, and the same value was adopted for the 15–30 cm layer. Bulk densities at P2lowWT were higher, at 0.17 g cm^{-3} in the 0–15 cm layer and 0.12 g cm^{-3} in the 15–30 cm layer.

The N_t contents at P1highWT were 9.3 g kg^{-1} (C/N = 48) in the upper layer and 8.8 g kg^{-1} (C/N = 54) in the lower layer. At P2lowWT they were 11.6 g kg^{-1} (C/N = 45) in the upper layer and 10.0 g kg^{-1} (C/N = 53) in the lower layer. Plant available NO_3^--N contents were not detectable in all samples. Mean plant available NH_4^+-N contents at P1highWT were 11.9 ± 6.2 mg kg^{-1} (2.0 ± 1.1 kg ha^{-1}) in the upper and 12.2 ± 6.6 mg kg^{-1} (2.1 ± 1.1 kg ha^{-1}) in the lower layer. Means at P2lowWT were 39.0 ± 12.7 mg kg^{-1} (9.9 ± 3.2 kg ha^{-1}) in the upper and 39.4 ± 22.5 mg kg^{-1} (7.2 ± 4.1 kg ha^{-1}) in the lower layer. Overall, NH_4^+-N contents at P2lowWT were three to four times higher than at P1highWT (Figure 5) and differences were statistically significant in both layers ($p \leq 0.01$).

Surface water and bog water chemistry

Surface water pH was on average 4.1 ± 0.2 at P1highWT and 4.1 ± 0.1 at P2lowWT. Average bog water pH was 4.0 ± 0.2 at P1highWT and 3.8 ± 0.1 at P2lowWT. NO_3^--N concentrations were not detectable in any of the samples. The range of NH_4^+-N concentrations in the surface water was 0.00–0.16 mg L^{-1} with a mean of 0.08 ± 0.06 mg L^{-1} at P1highWT, and 0.05–1.02 mg L^{-1} with a mean of 0.57 ± 0.30 mg L^{-1} at P2lowWT. The range of concentrations in the bog water was 0.01–0.71 mg L^{-1} with a mean of 0.16 ± 0.18 mg L^{-1} at P1highWT and 0.03–1.29 mg L^{-1} with a mean of 0.59 ± 0.39 mg L^{-1} at P2lowWT. So, in comparison with P1highWT, NH_4^+-N concentrations at P2lowWT were about seven times higher in the surface water and about four times higher in the bog water. Differences between the two sampling stations were statistically significant ($p \leq 0.01$). The concentrations in surface and bog water at P2lowWT peaked in spring and were lowest in autumn, while variations at P1highWT were negligible throughout the year except for an outlier in the bog water (Figure 6).

Vegetation

The highest N_t contents (dry mass basis) occurred in the wood of *Betula pubescens* (15.4 g kg^{-1} at P1highWT and 22.8 g kg^{-1} at P2lowWT) and in

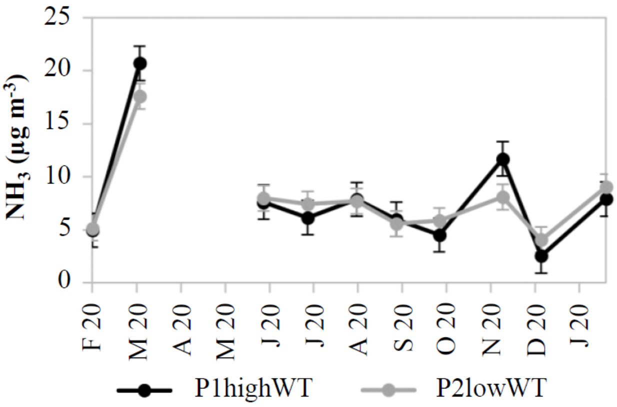

Figure 4. NH_3-N concentration in the ambient air. Whiskers indicate standard error. Data for April and May are missing because of a temporary laboratory closure.

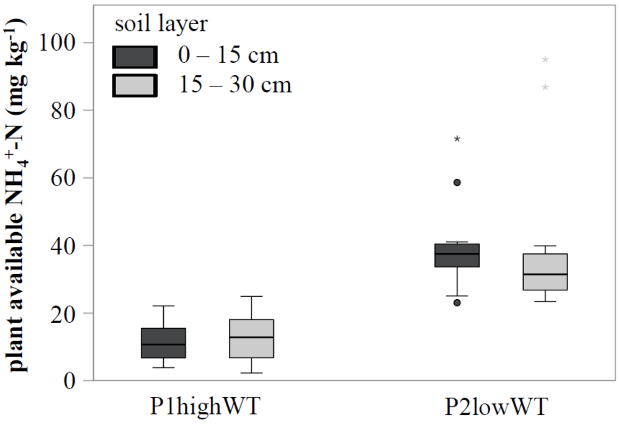

Figure 5. Contents of plant available NH_4^+-N in soil samples (dry mass basis) of the upper and lower soil layers. P1highWT: sampling station with mean water table 6 cm below ground surface; P2lowWT: sampling station with mean water table 17 cm below ground surface.

Molina caerulea (14.8 g kg^{-1} at P1highWT and 18.1 g kg^{-1} at P2lowWT) (Figure 7, Table 1). The mean contents were 11.6 ± 4.2 g kg^{-1} at P1highWT and 13.9 ± 4.9 g kg^{-1} at P2lowWT. Differences between the sampling stations were not statistically significant ($p > 0.05$). Considering the cover values for single plant species, the total amount of N_t stored in the vegetation of P1highWT was 23.2 kg ha^{-1}, with the greatest share of 7.77 kg ha^{-1} in *Sphagnum* spp. (e.g., *Sphagnum cuspidatum*, *Sphagnum fallax*). At P2lowWT the total amount of N_t stored in the vegetation was 29.6 kg ha^{-1} with the greatest share of 9.84 kg ha^{-1} in *Erica tetralix* (Figure 8, Table 1).

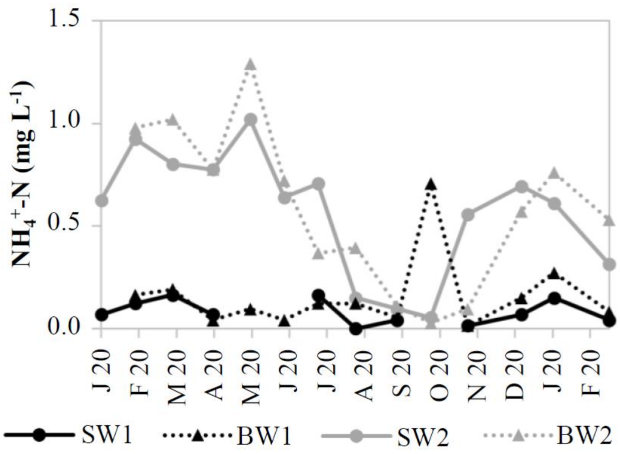

Figure 6. Concentrations of NH_4^+-N in water samples over the course of the year. SW1: surface water at P1highWT; SW2: surface water at P2lowWT; BW1: bog water at P1highWT; BW2: bog water at P2lowWT.

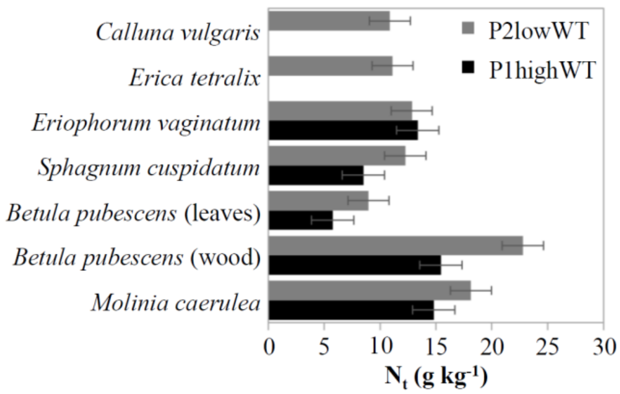

Figure 7. Total N content (dry mass basis) in single plant species. Whiskers indicate standard error. *Calluna vulgaris* and *Erica tetralix* did not occur at P1highWT.

DISCUSSION

N depositions

Our data confirmed the hypothesis that atmospheric N depositions into the Leegmoor would considerably exceed the CL of 5–10 kg ha^{-1} for natural bog ecosystems. The estimated total N deposition of 31.9 kg ha^{-1} y^{-1} with a large NH_3-N share of 18.2 kg ha^{-1} y^{-1} indicates that the Leegmoor receives high external input from the adjacent agricultural areas, even exceeding the CL of 15–25 kg ha^{-1} y^{-1} for degraded bogs such as the *Molinia caerulea* meadows investigated by Bobbink *et al.* (2015). The NH_3-N deposition is presumably not sufficiently considered in the modelled deposition value of 22 kg ha^{-1} y^{-1} for this area provided by UBA (2022). This may arise because the yearly atmospheric N input differs due to several effects, e.g., meteorological conditions or agricultural management, as shown by Hurkuck *et al.* 2014. Figures 4 and 6 show that both the NH_4^+-N and NO_3^--N concentrations in precipitation and the NH_3-N concentration of the ambient air peaked in spring, indicating an effect of manure application as shown in other studies (Hurkuck *et al.* 2014, McKenzie *et al.* 2016). Studies in the bog “Bourtanger Moor-Bargerveen” have shown that the greatest contributions to dry N deposition were produced by either local manure application (13 %) or long-distance transport (75 %), which resulted in a dry NH_3-N deposition of 9 kg ha^{-1} y^{-1} and a total N deposition of 25 kg ha^{-1} y^{-1} (Mohr *et al.* 2013, Hurkuck *et al.* 2014). The considerably higher total deposition in the Leegmoor results from the locally high dry NH_3-N deposition of 18 kg ha^{-1} y^{-1}, which is plausible because the Leegmoor study area lies in a region with one of the highest livestock densities in Germany (MU 2017, UBA 2022).

A limitation of the wet deposition data obtained for this study is that NO_3^--N and NH_4^+-N concentrations were not measured directly at the Leegmoor study site, but at the Sandkrug research site. However, comparison of data from Sandkrug with previous measurements in the Leegmoor (Köster 2016) over the same time period showed only a small deviation of about 5 % so that comparability can be assumed. In general, Mohr *et al.* (2005) showed that wet depositions in the rural areas of Northwest Germany are subject to rather small regional variation. This assumption is further supported by studies on the nearby bog “Tinner and Staverner Dose” conducted in 1993–1994 that reported mean wet N depositions of 6.9 kg NH_4^+-N ha^{-1} y^{-1} and 5.1 kg NO_3^--N ha^{-1} y^{-1} (TÜV 1995), which were slightly higher than our results but within a similar range.

Table 1. Measured attributes of vegetation (mean values), for calculation see Equation 1 in the Methods section. DM = dry mass, WC = water content (gravimetric), A = area sampled, s.a. = see above. Roots of *Molinia caerulea* were sampled at P1highWT only, and the results were extrapolated (*) to P2lowWT.

location	plant species	cover (%)	area (m^2)	DM (g)	WC (wt-%)	N_t in DM (g kg^{-1})	C/N	N_t in biomass (kg ha^{-1})	
P1highWT	*Molinia caerulea*	25	0.119	9.40	57.1	14.8	30	2.94	∑ = 20.0
	Betula pubescens (wood)	20	0.140	18.97	46.3	15.4	31	4.18	
	Betula pubescens (leaves)	s.a.	0.140	7.55	56.4	5.8	85	0.62	
	Sphagnum cuspidatum	30	0.010	3.04	96.7	8.5	52	7.77	
	Eriophorum vaginatum	25	0.030	3.94	56.5	13.4	33	4.47	
	Molinia caerulea (roots, 0–30 cm)	s.a.	0.160	24.54	77.4	6.61	69	2.53	∑ = 3.2
	Molinia caerulea (roots, 30–45 cm)	s.a.	0.160	9.50	72.1	4.60	99	0.68	
P2lowWT	*Molinia caerulea*	20	0.078	6.84	55.9	18.1	26	3.20	∑ = 27.0
	Betula pubescens (wood)	10	0.110	4.73	47.5	22.8	20	0.98	
	Betula pubescens (leaves)	s.a.	0.110	3.40	58.0	9.0	55	0.28	
	Sphagnum cuspidatum	10	0.010	3.38	92.9	12.3	36	4.14	
	Eriophorum vaginatum	10	0.047	2.60	55.1	12.8	35	0.72	
	Erica tetralix	25	0.040	14.18	43.7	11.1	48	9.84	
	Calluna vulgaris	25	0.040	11.54	46.9	10.9	46	7.85	
	Molinia caerulea (roots, 0–30 cm)	s.a.	s.a.	s.a.	s.a.	s.a.	s.a.	2.03*	∑ = 2.6
	Molinia caerulea (roots, 30–45 cm)	s.a.	s.a.	s.a.	s.a.	s.a.	s.a.	0.55*	

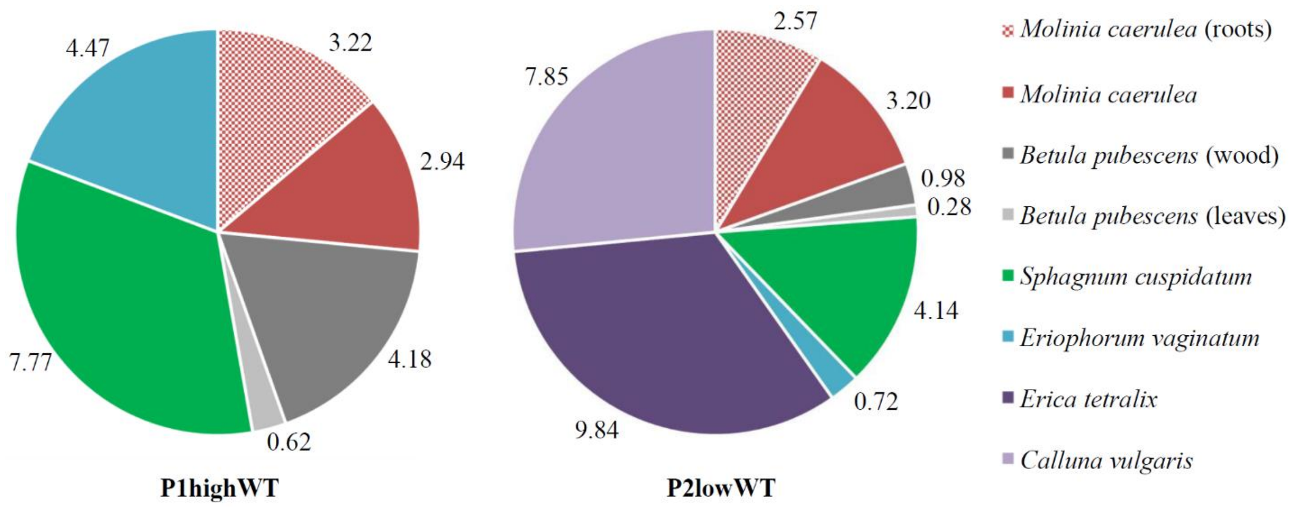

Figure 8. Total N storage (kg ha^{-1}) of plant species (shoots of plants unless otherwise specified).

Wet N depositions into the Leegmoor have decreased over recent decades. Between 1984 and 1988 they were as high as 27.1 kg ha^{-1} y^{-1}, accompanied by particularly high SO_4 depositions of 73 kg ha^{-1} y^{-1} (Nick *et al.* 1993) which facilitate formation of water-soluble ammonium sulphate, and have decreased strongly since that time. The decrease of wet N depositions is due to a decrease of acid compounds such as SO_2 and NO_x in the atmosphere, which promoted the deposition of basic NH_3 (Draaijers & Erisman 1995).

N uptake by the vegetation

The hypothesis that the vegetation incorporated significant amounts of excess N from atmospheric deposition was only partly confirmed. It was based on the knowledge that the vegetation cover newly developed on the bare peat after restoration, so nutrient legacy could be ruled out and we assumed that the emerging vegetation had a large nutrient uptake capacity.

Although N depositions into the Leegmoor exceeded the CL of 5–10 kg ha^{-1} for natural bog ecosystems and the CL of 15–25 kg ha^{-1} y^{-1} for *Molinia caerulea* meadows (Bobbink *et al.* 2015), the concentration of plant available N species in the bog water at P1highWT was low and stable throughout the year. Even when N depositions peaked in spring, there were no simultaneous or delayed peaks of NH_4^+-N concentrations in surface or bog water at P1highWT (Figures 3–5). The mean NH_4^+-N concentration in surface water at P1highWT was even below the maximum concentration of 0.1 mg L^{-1} that is to be expected in a natural bog (Bourbonniere 2009). This points towards relocation processes buffering the effects of high N depositions on the water N pool. In terms of soil N pools, experiments at Whim Bog (in Scotland) showed that extractable NH_4-N in the peat increased from about 50 µg g^{-1} under ambient deposition to about 250 µg g^{-1} under enhanced NH_3 deposition (Sheppard *et al.* 2013). Another study showed that experimental wet deposition of either NH_4^+-N or NO_3^--N at a rate of 32 kg ha^{-1} y^{-1} led to a three to four times increase of NH_4^+ concentration in pore water, while NO_3^- in the pore water was unaffected (van den Elzen *et al.* 2018). This indicated that pH and redox conditions characteristic of bog inhibited nitrification and, most importantly, that the uptake capacity of the vegetation was exceeded at this application rate. In our study, NH_4^+-N contents at P1highWT were clearly lower than the literature data, indicating that the capacity of the nutrient translocation processes was not (yet) reached.

However, invasion of *Molinia caerulea*, a strong indicator for the abundance of plant available N species, was observed over the last 30 years during which the average cover increased from 2 % to 40 % (Blankenburg *et al.* 2023). Many studies have reported that, apart from the influence of fluctuating water table (Gatis *et al.* 2019), high N depositions promote the growth of *Molinia caerulea* at the expense of many low-competitive bog species (e.g., *Sphagnum* spp., *Drosera* spp., *Eriophorum* spp.) by increasing N concentrations in the peat water (Limpens *et al.* 2003, Tomassen *et al.* 2003).

Examination of detailed species studies generally confirms that increase of tissue N content in bog plants occurs under high N depositions (e.g. Fritz *et al.* 2012, 2014). Chiwa *et al.* (2016) showed that after applying wet NH_4^+-N deposition rates of 56 kg ha^{-1} y^{-1} over a time span of 11 years, the tissue N concentration of the *Sphagnum* capitula rose from about 10 mg g^{-1} DM to 18 mg g^{-1} DM. In a study by Limpens *et al.* (2003) N contents of the *Sphagnum* capitula increased from 9.12 mg g^{-1} DM to 13.19 mg g^{-1} DM after a treatment with 40 kg N ha^{-1} y^{-1} over two growing seasons. In comparison with our study, N contents of the whole *Sphagnum* plant (8.5 mg g^{-1} DM) were relatively low at the wetter site P1highWT, indicating that the uptake capacity of *Sphagnum* was not exceeded yet. However, detailed statements about the annual N uptake capacity of *Sphagnum* cannot be made based on our data, as it remains unclear whether the sampled *Sphagnum* biomass developed solely over the course of the recorded time period.

Eriophorum N contents in the Leegmoor were 12.8 (P2lowWT) and 13.4 (P1highWT) mg g^{-1} DM, respectively, and high compared to the results of Limpens *et al.* (2003) who measured only a slight increased from 9.13 to 9.34 mg g^{-1} DM under N deposition of 40 kg ha^{-1} y^{-1}. Limpens *et al.* (2003) also showed that *Molinia caerulea* displayed a stronger increase of N contents than *Eriophorum*, from 8.04 mg g^{-1} DM to 10.50 mg g^{-1} DM. Likewise, in our study *Molinia* had comparatively high N contents of 14.8 (P1highWT) to 18.1 (P2lowWT) mg g^{-1} DM. Our findings suggest that *Molinia* incorporated a greater share of N and benefited more from high N levels than other bog-typical species. In contrast to bryophytes, which absorb N only from the surrounding air or in water directly via the tissue surface, higher plants like *Molinia caerulea* can take up N from the soil pore water (Dierssen & Dierssen 2008). At P2lowWT where NH_4^+ levels in the soil and bog water are relatively high, this is likely to provide a locational advantage for *Molinia caerulea* over bryophytes and to be an important factor in the annual N turnover.

Our data on the amount of N_t stored in the vegetation (23.2 kg ha^{-1} at P1highWT and 29.6 kg ha^{-1} at P2lowWT) (Table 1) are consistent with results obtained at the nearby bog complex "Bourtanger Moor / Bargerveen" by Mohr *et al.* (2013), who found that amounts of N in the above-ground biomass ranged between 19 and 40 kg ha^{-1} in three different bog biotopes dominated by young shrubs or trees, *Molinia* and *Eriophorum*, respectively. However, taking into account the discrepancy between the vegetation N pool of up to ~ 30 kg ha^{-1} and the determined N deposition of ~ 32 kg ha^{-1} y^{-1}, which is likely to be ~ 30 kg ha^{-1} y^{-1} or more over a long period of time, it has to be assumed that the current vegetation has incorporated only a small fraction of the N deposition. An imputed N deposition rate of 30 kg ha^{-1} y^{-1} over the last 40 years would have led to a gross N input of 1200 kg ha^{-1}, which shows that the whereabouts of a large part of the N deposited since the restoration about 40 years ago is unclear.

There are several other N translocation processes that were not determined in this study and are likely to have influenced the N dynamics. Firstly, an unknown amount of N was removed from the pool through landscape conservation measures like mowing of the study area after restoration. Depending on the vegetation type, ≥ 200 kg ha^{-1} of N can be removed by such conservation methods (Mohr *et al.* 2013). Secondly, there may be gaseous N losses as N_2 and N_2O through denitrification (van den Elzen *et al.* 2018). N emissions through N_2O efflux in European bogs reported in the literature range from low values of 1.0 kg ha^{-1} y^{-1} (Luan *et al.* 2019) or 1.1 kg ha^{-1} y^{-1} (Vybornova 2017) to 11.9 kg ha^{-1} y^{-1} (Oertel *et al.* 2016), and N_2 emissions may be even higher (van den Elzen *et al.* 2018). Thirdly, dissolved organic nitrogen (DON) in the bog water may increase under high N deposition and contribute up to 60–80 % to the total dissolved nitrogen (TDN), as opposed to a 20–40 % share of dissolved inorganic nitrogen (DIN) (Bragazza & Limpens 2004). Lastly, immobilisation of N in the peat may be a relevant process, as formation of new white peat was observed in some parts of the project area (Blankenburg *et al.* 2023). In growing bogs, the plant litter is only partially degraded, so N from the vegetation is partly immobilised in the soil organic N pool. Depending on the vegetation type, the amount of N in seasonal litterfall can vary between 4 kg ha^{-1} y^{-1} (*Eriophorum* spp.) and 32 kg ha^{-1} y^{-1} (*Betula* spp.) (Mohr *et al.* 2013). Estimates of N retained in North German growing bogs vary between 2.5 and 13.3 kg ha^{-1} y^{-1} per 1–2 mm of newly formed peat (DVGW 2020) or 65–75 % of deposited N (Frankl 1996, Dierssen & Dierssen 2008).

N release through peat mineralisation

Our data confirm the hypothesis that levels of plant available N in soil and water at the sampling station P2lowWT would exceed those at the sampling station P1highWT due to enhanced mineralisation. Besides mineralisation of peat and plant material by microorganisms, atmospheric deposition can be regarded as the most important N source for the plant available N pool. N depositions at the two sampling stations were practically equal and thus do not account for the differences in plant available N in soil and water between P1highWT and P2lowWT. The most striking difference between the sampling stations was that the average annual water level at P2lowWT was more than 10 cm lower than at P1highWT, which makes it likely that stronger mineralisation was responsible for the higher levels of plant available N. Mineralisation is generally promoted by aerated conditions resulting from water table drawdown (Munir *et al.* 2017).

Of the most crucial processes controlling the discharge of plant available N from the system, namely leaching, uptake by plants or microorganisms, immobilisation in the peat and denitrification (discussed above), leaching obviously played a subordinate role as bog water N levels at P1high WT were low. The C/N values are a reliable long-term indicator for mineralisation, are similarly large in both sites, and have remained mostly unchanged since restoration of the Leegmoor (C/N = 48 in the 0–15 cm layer and 56 in the 15–30 cm layer; Gebhardt & Knabke 1994). In forest soils with a raw humus layer, Gundersen *et al.* (1998) showed that atmospheric N depositions led to a continuous reduction of C/N values and increasing nitrification and nitrate leaching at C/N < 25. Other studies have demonstrated that the plant available N pool in peatlands is dominated by nitrate rather than ammonium after water table drawdown (Salonen 1994, Macrae *et al.* 2013). However, this was not the case in our study. It is unlikely that denitrification caused the differences in plant available N levels between the sampling stations, as the undetectable NO_3^- levels in both sites indicate similar redox potentials and high acidity (Dierssen & Dierssen 2008) in the soils throughout the study area, as already suggested in a previous study (Nachtigall & Giani 2022). Overall, the consistently large C/N values show that mineralisation is still hampered, but the elevated NH_4^+ level at P2lowWT compared to P1highWT is a strong indicator for mineralisation being the most likely process influencing the plant available N pool in terms of N recycling in areas with lower water table.

We assume that mineralisation was to some extent facilitated by water table fluctuations, in addition to average lower water table. The amplitude of fluctuations at P2lowWT was double that at P1highWT. Similar effects were discussed by Tfaily *et al.* (2018) who found that increased N turnover in bog soils related to fluctuating water table, and by Macrae *et al.* (2006) who linked elevated NH_4^+ and NO_3^- levels in bog soils to enhanced mineralisation through repeated drying and wetting. The water regime of rewetted bogs is strongly dependent, after water input through precipitation and water management through impounding, on the vegetation that controls water loss through evapotranspiration. Thus, water table fluctuations can be linked not only to climatic factors and water management but also to the eutrophication effect of high N depositions.

Implications for resilience and future management of the Leegmoor

Our results show that total N depositions on the Leegmoor bog greatly exceed the CL for bog ecosystems, giving reason to presume that the long-term survival of the remaining bog-typical plant species is at risk. The buffer capacity of the ecosystem was apparently not exceeded as concentrations of plant available N forms in the surface and soil water did not react to changes in atmospheric N deposition. On the other hand, the tissue N_t contents of *Eriophorum vaginatum* and *Molinia caerulea* were elevated and typical for bogs with higher N deposition. The same was true for the N_t pool stored above-ground in the vegetation. Although the N storage capacity of the vegetation was high, uptake of N by plants did not sufficiently explain the relatively low levels of plant available N forms in the water and soil pools. Other possible contributing processes involve N removal by mowing, denitrification or immobilisation in the peat and should be the subject of future research. We conclude that the buffering capacity of the ecosystem may at some point be surpassed and the overall N status of the ecosystem will then deteriorate. To date, enhanced mineralisation, especially ammonification, under lower water table and stronger water table fluctuations, had a greater influence on the availability of plant available NH_4^+ in the water and soil than did N depositions. This shows that water management is crucial for the restoration and preservation of bogs which is, however, cross-influenced by the eutrophication effect of high N deposition that becomes evident in the dominance of *Molinia caerulea*. The stable C/N values over time are an indication for soil chemical resilience of the bog, despite its unfavourable restoration conditions on black peat. However, the vegetation showed some symptoms of eutrophication, indicating that this situation might change in the future. Consequently, apart from appropriate water management, the reduction of atmospheric N depositions is a crucial factor for achieving the goal of sustainable bog restoration.

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AUTHOR CONTRIBUTIONS

SN, LG and KM conceptualised the study. Data/sample collection and analyses were performed by SN except for the precipitation N concentration data which were collected by KM. All versions of the manuscript were written by SN and revised by LG and KM. All authors approved the final manuscript.

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