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Gaseous nitrogen losses and mineral nitrogen transformation along a water table gradient in a black alder (*Alnus glutinosa* (L.) Gaertn.) forest on organic soils

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Abstract

Black alder (*Alnus glutinosa* (L.) Gaertn.) forests on peat soils have been reported to be hotspots for high nitrous oxide (N_2O) losses. High emissions may be attributed to alternating water tables of peatlands and to the incorporation of high amounts of easily decomposable nitrogen (N) into the ecosystem by symbiotic dinitrogen (N_2)-fixation of alder trees. Our study addressed the question to what extent drainage enhances the emissions of N_2O from black alder forests and how N turnover processes and physical factors influence the production of N_2O and total denitrification. The study was conducted in a drained black alder forest with variable groundwater tables at a southern German fen peatland. Fluxes of N_2O were measured using the closed chamber method at two drained sites (D-1 and D-2) and one undrained site (U). Inorganic N contents and net N mineralization rates (NNM) were determined. Additionally a laboratory incubation experiment was carried out to investigate greenhouse gas and N_2 fluxes at different temperature and soil moisture conditions. Significantly different inorganic N contents and NNM rates were observed which however did not result in significantly different N_2O fluxes in the field, but in the laboratory experiment. Measured N_2O fluxes were low for all sites, with total annual emissions of 0.51 ± 0.07 (U), 0.97 ± 0.13 (D-1) and 0.93 ± 0.08 kg N_2O-N ha^{-1} yr^{-1} (D-2). Only 37 % of the spatio-temporal variation in field N_2O fluxes could be explained by peat temperature and groundwater level, demonstrating the complex interlinking of the controlling factors for N_2O emissions. However, temperature was one of the key variables of N_2O fluxes in the conducted incubation experiment. Increasing soil moisture content was found to enhance total denitrification losses during the incubation experiment, whereas N_2O fluxes remained constant. At the undrained site, permanently high ground water level was found to prevent net nitrification, resulting in a limitation of available nitrate (NO_3^-) and negligible gaseous N losses. Up to four times higher N_2O flux rates were measured in the incubation experiment. They reveal the potential of high N_2O losses under changing soil physical

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conditions at the drained alder sites. The observed high net nitrification rates and high NO_3^- contents bear the risk of considerable NO_3^- leaching at the drained sites.

1 Introduction

Black alder (*Alnus glutinosa* (L.) Gaertn.) forests represent the natural vegetation in many semi wet and wet regions mostly on soils with high organic carbon contents (Dilly et al., 1999; Kätzel, 2003; Schäfer and Joosten, 2005). Unlike most other wetlands, alder forests on peatland represent non N-limited ecosystems, due to the ability of alder trees for symbiotic N_2-fixation of up to 85 kg N ha^{-1} yr^{-1} (Dittert, 1992; Augustin, 2003). Up to date, there are only a few studies on N-turnover and N-transformation processes in black alder forests on peatland. First results indicate that these ecosystems show high N-transfer rates between the atmosphere, the alder trees and the soil (Augustin, 2003). Through the symbiotic N_2-fixation high amounts of easily decomposable N enter the ecosystem and lead to a low C/N ratio of the soil organic matter (Lõhmus et al., 2002). Semi wet peat soils with low C/N ratios are known to be potential hotspots for gaseous and dissolved nitrogen losses via mineralization, nitrification, denitrification and nitrate leaching (Lõhmus et al., 2002; Gundersen et al., 1998; Ollinger et al., 2002; Klemedtsson et al., 2005). Particularly, enhanced N_2O emissions are of great interest due to the fact that N_2O acts as radiative forcing greenhouse gas (IPCC, 2007) and contributes to the chemical destruction of stratospheric ozone (Crutzen, 1979). The few annual observations of N_2O emissions from *Alnus* forest ecosystems on drained or undrained peatlands range between 0.1 and 72.0 kg N ha^{-1} yr^{-1} (Augustin et al., 1998; Brumme et al., 1999; Merbach et al., 2001; von Arnold et al., 2005). Most emissions exceed by far the IPCC default emission factor of 0.6 (0.16–2.4) kg N_2O-N ha^{-1} yr^{-1} (IPCC, 2006) for boreal and temperate nutrient-rich forest peatlands. The high range requires in-depth process understanding to narrow down the uncertainty and better understand N_2O formation, not at least because of the attempt to reduce the climate impact of drained fen peatland by rewetting and afforestation with black alder trees

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(*Alnus glutinosa* (L.) Gaertn.) (Schäfer and Joosten, 2005; Wichtmann and Joosten, 2007).

The production of N_2O depends mainly on the two microbial processes of denitrification and nitrification (Davidson, 1986). Thus, the availability of soil mineral N and oxygen are the main controlling factors (Del Grosso et al., 2000; Jungkunst et al., 2004). Highest N_2O fluxes are mainly related to incomplete denitrification. This requires the presence of efficient electron acceptors (e.g. NO_3^-) to prevent the reduction of N_2O to N_2 (Bremner and Blackmer, 1981; Speir et al., 1995; Jungkunst et al., 2004). Due mainly to analytical difficulties in the determination of microbially produced N_2, up to date the denitrification potential from waterlogged peat soils has rarely been estimated (Watts and Seitzinger, 2000; Mander et al., 2003; Teiter and Mander, 2005; Wray and Bayley, 2007; Roobroeck et al., 2010; Soosaar et al., 2011; Uri et al., 2011). The substitution of ambient N_2 by Helium (He) in laboratory studies possibly represents the most reliable method for the direct and simultaneous determination of N_2O and N_2 exchange rates (Butterbach-Bahl et al., 2002; Roobroeck et al., 2010; Butterbach-Bahl et al., 2013).

The objectives of our study were to quantify (i) the nitrogen mineralization and nitrogen transformation processes, and (ii) N_2O emissions and the factors regulating the N_2O emissions and N_2O/N_2 ratio along a soil moisture gradient in black alder forest on organic soil.

We hypothesize that (1) in drained black alder forests high N_2O emissions occur due to accelerated N turnover and N mineralization, and (2) N_2O is replaced by N_2 losses during periods of temporarily high water levels. In contrast, NO_3^- limitation in permanently waterlogged peat soils results in negligible N_2O and N_2 losses. To investigate our hypotheses, we selected three sites in an alder forest along a groundwater table gradient, representative for the small-scale heterogeneity of the forest stand.

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2 Materials and methods

2.1 Study area and experimental design

The study was carried out in a drained 45 yr-old black alder (*Alnus glutinosa* (L.) Gaertn.) forest stand (2.2 ha) on organic soil (Freisinger Moos, 48°22′ N, 11°40′ E; 449 m a.s.l.). According to the climate station in Weihenstephan, located 10 km north-east of the sites, the 30 yr mean annual temperature was 7.5 °C and the mean annual precipitation was 787 mm (1961–1990). At a German Level II monitoring area, located in 5 km distance to the alder forest, annual stand N deposition amounted to 17.67 kg N ha^{-1} yr^{-1} with a NH_4^+-N : NO_3^--N ratio of 46 : 54 in 2011 (data were collected and analysed by the Bavarian State Institute of Forestry). Approximately 15 % of the forest area is covered by undrained hollows whereas most parts are drained by ditches. In October 2009, we selected three sites which differed in groundwater table (Table 1). In parallel, the sites also differed in other soil factors relevant for N_2O processes, such as bulk density, carbon and nitrogen content (Table 2). One site was placed in an undrained hollow (named U). The other two sites were placed at the drained part of the forest (named D-1 and D-2) along a gradient of drainage depth. Soils at the drained sites were classified as sapric Histosols whereas the undrained site was classified as Fluvisol (according to WRB, 2006). The surface organic layer at the drained sites was a L-mull humus and formed a submerged mud layer at the undrained site. The black alder stand was planted on grassland in 1965 and has not been managed. In 2009, stem density was approximately 1031 trees per hectare, with a mean height of 19.7 m and a mean diameter in breast height of 21 cm (Röhling, personal communication). At the site U, the dominant species in the herb layer were *Phragmites australis* and *Carex acutiformis*. Site D-1 was dominated by *Impatiens glandulifera, Impatiens parviflora, Deschampsia cespitosa* and *Circaea x intermedia*, whereas site D-2 was dominated by *Carex acutiformis, Circaea x intermedia, Rubus caesius* and *Carex elongata*.

At each site, three PVC-collars for GHG measurements (inside dimension 75 × 75 cm) were permanently inserted 10 cm into the soil. Collars of a site were grouped closely

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to each other (distance between 0.8 and 2.5 m) due to large heterogeneity in soil properties. Boardwalks were installed to prevent oscillations of the peat through movements during the measurements. Plastic perforated tubes (JK-casings DN 50, Ø 60 mm, length 1 m) were installed close to each collar for plot-specific measurements of groundwater table during gas flux measurements. We equipped one tube per site with a water level logger (Type MiniDiver, Schlumberger water services), which logged the water table every 15 min. Additionally, climate stations were installed between the sites D-1 and D-2 at the beginning of March 2010 and at site U in April 2011. At each climate station, air temperature and humidity at 20 cm above soil surface, soil temperatures at depth of −2, −5 and −10 cm as well as soil moisture content at −5 cm were logged every 30 min. Additional to the recorded data, site-specific soil temperatures in three soil depths (−2, −5 and −10 cm) were determined with penetration thermometers at the beginning and end of each gas flux measurement. Moreover, plot-specific groundwater levels were measured inside the tubes without loggers during gas flux measurements.

2.2 Field measurements

2.2.1 N_2O flux measurements

We measured fluxes of N_2O every second week from December 2010 to January 2012 using the static manual chamber method with chamber height of 0.5 m (Livingston and Hutchinson, 1995). At site U, in periods where the forest floor vegetation grew higher than the chamber height, extensions (same dimension as chamber) were installed between the collar and chamber (white, opaque, volume varied between 309 and 927 L). A detailed description of chamber dimension and configuration is given in Drösler (2005). Four gas samples were taken at four regular time intervals after chamber closure (enclosure time 60 min, in case of two extensions 120 min). The samples were collected in 20 mL glass vials, each sealed with a butyl rubber septum. The vials were flushed with chamber air for 30 s using a portable micro pump (KNF Neuberger GmbH, NMP015B), so that the air in the vials was exchanged 32 times. In addition

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the pump was used to build up an overpressure of approximately 550 mbar to protect the sample against fluctuations in atmospheric pressure during storage. Gas analyses were carried out with a gas chromatograph (Perkin and Elmer, Clarus 400 GC respectively Clarus 480 GC) equipped with a headspace auto sampler (Perkin and Elmer,TurboMatrix 110), a PoraPack 80/100 mesh column and an electron capture detector (ECD) for N_2O (ECD temperature 380 °C). Gas flux rates were calculated from the linear change in gas concentration over time considering chamber air temperature and atmospheric pressure. Gas fluxes were accepted when the linear regression was significant ($P \leq 0.05$). In case of small N_2O fluxes, fluxes were also accepted if the coefficient of determination was ≥ 0.90 and the regression slope was between −1 and 1 ppb min^{-1}. The cumulative annual mean exchange rate was calculated by linear interpolation between the measurement dates.

2.2.2 Soil sampling and laboratory analysis

Total carbon (C_{tot}), organic carbon (C_{org}) and total nitrogen (N_{tot}) were analysed by the AGROLAB Labor GmbH (Bruckberg, Germany) on three mixed soil samples per site. Each sample was composed of nine individual samples collected close to each collar at two soil depths (0–10, 10–20 cm). After drying for 72 h at 40 °C, soil samples were sieved to 2 mm to remove stones and living roots.

For the determination of bulk density and porosity, three undisturbed core cutter samples (100 cm^3) were randomly taken at four depths (0–5, 5–10, 10–15, 15–20 cm) for each site.

During every gas flux measurement, one mixed soil sample consisting of nine individual samples was collected at two soil depths (0–10, 10–20 cm) for each site for the determination of mineral N (N_{min} = NH_4^+-N + NO_3^--N) contents. Samples were immediately cooled in an ice box up to the further processing. Mineral N was extracted after shaking 40 g of fresh soil with 160 mL $CaCl_2$ (0.0125 M) for one hour. The extracts were filtered through a 4–7 µm filter paper (Whatman 595 1/2) and the first 20 mL of the extract were discarded. The solution was frozen at −20 °C until analysis, which

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was conducted by the AGROLAB Labor GmbH (Bruckberg, Germany). A subsample of 20–30 g was used to determine the gravimetric water content, which was taken into account for the calculation of mineral N concentrations.

2.2.3 Net N mineralization

In 2011, net ammonification, nitrification and N mineralization rates (NNM) were determined in situ in four different periods in time (March, June, September and December). At each study site and period, three pairs of intact soil cores were taken randomly from the upper 20 cm of the soil layer using a cylindrical auger (diameter of 45 mm). In case of flooding at the undrained site, disturbed soil samples were used. One core of each pair was sealed in low density polyethylene (LDPE) bags (19 µm) and returned into the soil for incubation (t1), which lasted 21 days (20 days in December) (e.g. Adams et al., 1988). The other soil cores were used as initial samples (t0). Mineral N contents were determined as described before after soil cores were divided into 0–10 and 10–20 cm sections. Net ammonification, net nitrification and net N mineralization were calculated according to the method described by Uri et al. (2003).

2.3 Laboratory incubation experiment

In June 2011, four intact soil cores with a diameter of 7.3 cm and a height of 6 cm were collected from the soil depth 9–15 cm close to each collar of the site D-2 for incubation in the laboratory. The samples were immediately weighed and stored at 4 °C. Four additional intact soil cores were taken to determine the gravimetric water content and estimate the water filled pore space (WFPS). This information was used to adjust the WFPS in the cores for laboratory incubation to 70 % and 100 % (two replicates for each WFPS per collar; six replicates per site). Due to a WFPS of approximately 100 % at the site U, only the two soil cores per collar for incubation at WFPS of 100 % and the cores for determination of water content were directly collected in the field and were treated as the samples from site D-2. Additionally, three cubic blocks (di-

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mension 40 × 25 cm, height 20 cm) were collected with plastic containers where the bottom plate was removed before, in order to prevent shrinking losses in the cores by drying to 70 % WFPS. For transport, storage and drying, the containers where placed on perforated metal plates. Six intact soil cores for site U where collected from these soil blocks after they reached the required 70 % WFPS. For measurements of N_2, N_2O, CO_2 and CH_4 fluxes, we applied the helium-oxygen (He-O) method (Butterbach-Bahl et al., 2002; Mander et al., 2003; Roobroeck et al., 2010; Uri et al., 2011) using four different incubation temperatures (0, 5, 15 and 25 °C). Five replications per site and moisture content were simultaneously placed in special gas-tight incubation vessels inside a climate chamber. The sixth one served as a reserve. Analyses were conducted in the laboratory of the Institute of Landscape Matter Dynamics, Leibniz Centre for Agricultural Landscape Research (ZALF), Müncheberg, Germany. Four substitution sequences with moderate evacuation (0.047 bar) followed by flushing the vessels with an artificial He/O_2 gas mixture (20.58 % O_2, 347.8 ppm CO_2, 1.780 ppm CH_4, 0.290 ppm N_2O, 3.04 ppm N_2, rest He) were conducted to remove ambient N_2. Subsequently, the air temperature of the climate chamber was set to 0 °C and a continuously He/O_2 gas flow rate of 15 mL min^{-1} was adjusted to the vessel headspaces, followed by a 24 h period to establish a new flow equilibrium. From each vessel, we measured the N_2O, CO_2 and CH_4 headspace concentration once and the N_2 concentration three times. After gas flux measurements were done, we immediately increased the incubation temperature to the next level for 20 h and continued the measurements. Soil core samples lost approximately 5.0 ± 0.9 % and 2.7 ± 0.3 % of their initial water content at 100 % and 70 % WFPS during the incubation procedure of 5 days. Concentration of N_2 were analyzed by a micro-GC (Agilent Technologies, 3000 Micro GC), equipped with a thermal conductivity detector (TCD). Gas chromatograph settings were: TCD temperature 60 °C, sample inlet 60 °C, molsieve capillary column (14 m), oven temperature 60 °C, carrier gas, He/O_2 6.0 (15 mL min^{-1}). Concentration of trace gases were analyzed by a GC (Shimadzu, Duisburg, Germany, GC-14B) equipped with a FID for CH_4 and an ECD for N_2O and CO_2. GC settings were: FID temperature 310 °C, ECD tem-

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perature 310 °C, column PoraPack 80/100 mesh, oven temperature 60 °C, carrier gas, N_2 6.0 (13 mL min^{-1}). Flux rates were calculated from the actual gas concentration of the continuous flow rate from the vessels headspace after subtraction of a blank value from a vessel without a soil core, which is equivalent to concentrations from the artificial He/O_2 gas mixture. After incubation the WFPS of the soil cores was determined to test the accuracy of the adjusted WFPS. The samples from site U and D-2 had exactly 100 % WFPS as well as D-2 at 70 % WFPS (on average 70.4 ± 2.2 % WFPS). For site U, however, WFPS had been adjusted to 83.0 ± 0.5 % WFPS instead of 70 %. In order to obtain the temperature effect on gas flux rates, Q_{10} values were calculated from the following equation:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\left(\frac{10}{T_2 - T_1}\right)} \quad (1)$$

where Q_{10} is the temperature quotient; R_1 and R_2 are gas flux (CO_2, CH_4, N_2O, N_2) rates (mg C or N m^{-2} h^{-1}; µg C or N m^{-2} h^{-1}); T_1 and T_2 are temperature (°C).

2.4 Statistical analysis

Statistical analyses were conducted using R 2.12.1 (R Development Core Team 2010). The assumption of normality of residuals was tested using the Lilliefors or Shapiro–Wilk test and by plotting the Quantile–Quantile plots. Homogeneity of variances of residuals was checked with the Levene or Breusch–Pagan test and by plotting the residuals against the fitted values. If necessary, data were transformed (Box–Cox) prior to analyses. We used analysis of variance (ANOVA) (for NNM rates) or the nonparametric Kruskal–Wallis Rank Sum test (for WFPS, NO_3^-, NH_4^+) to compare means of samples. In case of significant differences among the means, we used Tukey's honest significant differences (TukeyHSD) or the non-parametric Pairwise Wilcoxon Rank Sum test with Bonferroni correction for multiple comparisons. For testing two independent sample means (for WFPS, NO_3^-, NH_4^+), we used the non parametric Mann–Whitney U test.

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Due to temporal pseudoreplication of time series data (N_2O field measurements) and repeated measurements of vessels in the incubation experiment we applied linear mixed effect models (Crawley, 2007; Eickenscheidt et al., 2011; Hahn-Schöfl et al., 2011). For N_2O field measurements we set up a basic model with site type as fixed effect and the spatial replication (individual plot) nested in time as random effect. For the incubation experiment (N_2O, N_2, CO_2, CH_4), the fixed structure included the temperature, the site type and the soil water filled pore space as well as all possible interaction terms. Non significant terms were removed from the fixed structure. The individual vessel was set as random effect. We extended the respective basic model by a variance function when heteroscedasticity was observed. In case of significant serial correlation in data, a first-order temporal autoregressive function was included in the model. Autocorrelation was tested with the Durbin–Watson test and by plotting the empirical (partial) autocorrelation structure (Eickenscheidt et al., 2011). The model extension was proven by the Akaike Information Criterion (AIC). For multiple comparisons, we conducted Tukey contrasts using the General Linear Hypotheses function from the "multcomp" package (Hothorn et al., 2013). We used non-linear regressions to explain field N_2O fluxes and NNM rates. The model structure for mean N_2O fluxes included a linear term for the soil temperature in −2 cm soil depth and a cubic term for the mean GW level. Serial autocorrelation was not taken into account in the regression model. The non-linear model for NNM rates was optimized by using the program Table Curve 3-D (version 4.0) (non-linear equation is shown in Fig. 4). We accepted significant differences if $P \leq 0.05$. Results in the text are given as means ±1 standard error.

3 Results

3.1 Site characteristics

In 2011, the forest air temperature in 20 cm height ranged from −12.3 to 27.8 °C with an annual mean of 9.1 °C. Soil temperature in −2 cm soil depth averaged 9.6 °C at the

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drained sites and was slightly lower with 9.2 °C at the undrained site. The topsoil at the undrained site U consisted of a mud sediment while the topsoil at the drained sites D-1 and D-2 consisted of highly degraded fen peat. Total organic carbon and the total nitrogen concentrations in the 0–10 cm and 10–20 cm soil layers were 2 to 3 times higher at site U than at sites D-1 and D-2 (Table 1 and Table 2). Due to much higher bulk density, however, the total N stock in the upper 20 cm of the soil was more than 50 % higher at D-1 and D-2 than at U. The C/N ratios of all sites were narrow (between 11 and 16), indicating nitrogen-rich conditions. No relation between soil properties and N fluxes was determined so that the results and discussion focus on groundwater table and climate variables.

The three sites showed similar dynamics in their annual hydrographs but on different levels (Fig. 1). The mean annual groundwater level was +4 cm at U, −40 cm at D-1, and −47 cm at D-2. At site U, WFPS remained permanently close to 100 %. At the drained sites, WFPS was close to 70 % (D-1) and 63 % (D-2) in the 0–10 cm layer and around 80 % in the 10–20 cm layer with some temporal variation (Table 1).

3.2 Nitrogen availability and net N mineralization

In 2011, extractable NO_3^- contents in both investigated soil depths significantly differed among the three sites (all $P < 0.03$) (Table 1). At the undrained site, most of the time nitrate was not detectable, whereas the drained sites showed high NO_3^- contents (Fig. 2a), in particular for the soil depth 10–20 cm. However, differences between the two soil depths were not significant.

In contrast to NO_3^-, significantly higher NH_4^+ contents were measured at the undrained site than at the drained sites (Table 1). NH_4^+ contents did not significantly vary between soil depths.

In line with the high contents of extractable inorganic N compounds, NNM rates were also high at the drained sites (Fig. 3a and b). For both soil depths, the drained sites had significantly (all $P < 0.005$) higher NNM rates than the undrained site whereas differences between the drained sites were not significant. The NNM rates decreased with

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soil depth, but differences were not statistically significant. The mean NNM rates of the four investigated time periods and the upper 20 cm of the soil were $23 \pm 7\,mg\,N\,m^{-2}\,d^{-1}$ (U), $179 \pm 35\,mg\,N\,m^{-2}\,d^{-1}$ (D-1) and $142 \pm 32\,mg\,N\,m^{-2}\,d^{-1}$ (D-2). Assuming that the time periods are representative for the annual dynamics, mean annual NNM rates are estimated to be $84 \pm 26\,kg\,N\,ha^{-1}\,yr^{-1}$ (U), $653 \pm 128\,kg\,N\,ha^{-1}\,yr^{-1}$ (D-1) and $518 \pm 117\,kg\,N\,ha^{-1}\,yr^{-1}$ (D-2). The NNM rates of the upper 10 cm displayed a clear seasonality with high rates during the summer months and low rates during the winter months. However, only in June a significantly (all $P < 0.001$) higher NNM rate was observed compared to December and March. At the drained sites, net nitrification amounted to nearly 100 % of the NNM whereas ammonification was the dominating process at the undrained site. Negative net nitrification rates (NO_3^- consumption) were detected at the undrained site in June and September in 0–10 cm soil depth. The NNM in the upper 10 cm of the soil depended on the WFPS and the mean temperature in −5 cm soil depth (Fig. 4).

3.3 Field N_2O fluxes

Annual N_2O emissions were unexpectedly low at all three sites (Fig. 5c) with $0.51 \pm 0.07\,kg\,N\,ha^{-1}\,yr^{-1}$ (U), $0.97 \pm 0.13\,kg\,N\,ha^{-1}\,yr^{-1}$ (D-1) and $0.93 \pm 0.08\,kg\,N\,ha^{-1}\,yr^{-1}$ (D-2). The differences in N_2O fluxes between the sites were not statistically significant. At the drained sites the highest N_2O emissions were observed during the late summer and autumn, whereas at the undrained site highest emissions occurred during the dry period in May (Fig. 1d, 2d). The temperature at −2 cm soil depth and the mean groundwater level showed the best explanatory power for mean N_2O fluxes; nevertheless only 37 % of the spatio-temporal variation could be explained ($P < 0.001$). Site-specific regression analyses explained 55 % of temporal N_2O variation at D-1 ($P < 0.001$), 32 % at D-2 ($P < 0.01$) and 20 % at U ($P < 0.04$).

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3.4 Effect of temperature and soil moisture on greenhouse and dinitrogen gas exchange under laboratory conditions

3.4.1 CO_2 exchange

CO_2 exchange indicates heterotrophic soil respiration in the incubation. No significant effect of soil moisture and site type on CO_2 exchange was detected (Fig. 6a), indicating comparable soil microbial activity in all incubated treatments. A statistically significant ($P < 0.0001$) quadratic effect of temperature on CO_2 emissions was observed in all treatments with Q_{10} values between 1.82 and 17.80 mg C m^{-2} h^{-1} 10 °C^{-1}.

3.4.2 CH_4 exchange

No significant CH_4 emissions were observed in any treatment (Fig. 6b). Incubations at 100 % WFPS showed consistent near zero CH_4 fluxes or slight CH_4 uptake without significant effects of site type and temperature. At 70 % WFPS the uptake of CH_4 was significantly ($P < 0.0001$) higher at all temperature levels and for both sites compared to 100 % WFPS. CH_4 uptake increased significantly with temperature only in incubated samples of the drained site ($P < 0.001$). The CH_4 data indicate that the samples were aerobic at 70 % WFPS and only slightly anaerobic at 100 % WFPS so that the samples were incubated at conditions favorable for denitrification but not for methanogenesis.

3.4.3 N_2O exchange

N_2O exchange differed in response to site type, WFPS and temperature. Significantly ($P < 0.0001$) higher N_2O fluxes at both WFPS levels were measured from samples of the drained site (D-2) compared to samples from the undrained site (U) (Fig. 6c). At the drained site, Q_{10} of N_2O emissions was 2.17 µg N m^{-2} h^{-1} 10 °C^{-1} at 70 % WFPS for the temperature range of 0 to 25 °C and 2.12 µg N m^{-2} h^{-1} 10 °C^{-1} at 100 % WFPS for 0 to 15 °C.

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For both WFPS levels, samples of the undrained site (U) only showed a weak, but significant (all $P < 0.03$) temperature response for the temperature range of 0 to 15 °C. The Q_{10} values of N_2O emissions for the undrained site were 2.07 µg N $m^{-2} h^{-1}$ 10 $°C^{-1}$ at 100 % WFPS for 0 to 15 °C and 1.51 µg N $m^{-2} h^{-1}$ 10 $°C^{-1}$ at 70 % WFPS for 0 to 25 °C.

For both sites a decline in nitrous oxide emissions at 25 °C and 100 % WFPS was observed. However, this pattern was also detected at 70 % WFPS for the undrained site. Observed N_2O emissions at the undrained site U were in the same order of magnitude as the field measurements, whereas the drained site D-2 samples showed up to four times higher N_2O fluxes during the laboratory incubation than in the field at 70 % WFPS.

3.4.4 N_2 exchange

N_2 emissions were near zero at 70 % WFPS at low temperatures and never exceeded 0.4 mg N $m^{-2} h^{-1}$ at high temperatures. N_2 emissions at 100 % WFPS were consistently at least 10 times higher than at 70 % WFPS ($P < 0.0001$). N_2 exchange also reacted to site type at 25 °C, and to temperature. At the drained site, Q_{10} of N_2 emissions was 2.03 µg N $m^{-2} h^{-1}$ 10 $°C^{-1}$ at 70 % WFPS for the temperature range of 0 to 25 °C and 1.48 µg N $m^{-2} h^{-1}$ 10 $°C^{-1}$ at 100 % WFPS for the temperature range of 5 to 25 °C. At the undrained site, Q_{10} of N_2 emissions was 2.13 µg N $m^{-2} h^{-1}$ 10 $°C^{-1}$ at 70 % WFPS for the temperature range of 0 to 25 °C. N_2 emissions of the undrained site did not respond to temperature at 100 % WFPS. N_2 emissions increased most strongly from 15 °C to 25 °C in samples of the drained site at 70 % and in particular 100 % WFPS and in samples of the undrained site at 70 % WFPS.

The observed high N_2 emissions at 100 % WFPS resulted in low N_2O/N_2 ratios, with mean values of 0.03 ± 0.01 (U) and 0.10 ± 0.02 (D-2). A similarly low N_2O/N_2 ratio (mean value of 0.12 ± 0.03) was found at 70 % WFPS for the samples from the U site, as a result of the low N_2O emissions. In contrast, the samples from the drained site D-2

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showed a considerably higher N_2O/N_2 ratio, with a mean value of 0.62±0.11 (note that in case of zero N_2 fluxes no ratio was calculated). A relationship between temperature and N_2O/N_2 ratio was not observed for both soil moisture contents.

4 Discussion

4.1 Nitrogen mineralization and transformation processes

For both drained sites, the observed NNM rates are at the high end of NNM rates given in the literature. Janiesch (1978) and Janiesch et al. (1991) reported NNM rates of up to 500 $kg\,ha^{-1}\,yr^{-1}$ (0–15 cm soil depth) and of up to 321.2 $kg\,ha^{-1}\,yr^{-1}$ (0–10 cm soil depth) for different *Alnus glutinosa* forests from degraded fen peatlands in northern Germany. The significantly lower NNM rates from the undrained site are in the range of NNM rates reported for other semi-natural black alder forests (Janiesch, 1978; Janiesch et al., 1991).

The compiled values from the literature and the results of the present study indicate an increasing NNM rate in black alder forests with increasing degradation of the fen peatland. In forest soils, high NNM rates are generally related to narrow C/N ratios (Gundersen et al., 1998; Ollinger et al., 2002), which are also characteristic for alder swamps (Mäkinen, 1979) and which were observed in the present study. Typically NNM rates for deciduous stands range between 50–150 $kg\,N\,ha^{-1}\,yr^{-1}$ (Aber et al., 1989). The considerably higher NNM rates measured in the present study compared to other deciduous forests can partly be attributed to the high amount of easily decomposable organic nitrogen which becomes incorporated into the forest ecosystem through symbiotic atmospheric N_2 fixation by *Frankia* actinomycetes (Kätzel, 2003). Dittert (1992) estimated N_2 fixation rates between 40–85 $kg\,N\,ha^{-1}\,yr^{-1}$ for a black alder stand in northern Germany. Comparable and even higher values have also been reported for grey alder stands (e.g. Rytter et al., 1991; Lõhmus et al., 2002; Mander et al., 2005; Uri et al., 2011). Additionally, drainage of histosols supplies large amounts of N through

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mineralization of ancient organic matter (Klemedtsson et al., 2005). Low retranslocation of nitrogen from senescing leaves to the alder tree (Mander et al., 1997; Lõhmus et al., 2002; Uri et al., 2011) causes high contents of N and narrow C/N ratios of the foliage, favoring the fast decomposition of the leaf litter (Struwe and Kjøller, 1990; Ryter et al., 1991; Lõhmus et al., 2002; Uri et al., 2011). The organic surface layer at the drained sites was classified as L-mull humus type, indicating the fast decomposition of the incorporated alder leaves.

Beside substrate chemistry, moisture content together with temperature are considered as the most important abiotic factors influencing biogeochemical transformation processes (Tietema et al., 1992). In general, increasing moisture contents stimulate the biogeochemical processes, up to a threshold value where anaerobicity can limit microbial activity (Tietema et al., 1992). Temperature has a similar effect on microbial activity, due to the fact that rates of enzymatic processes generally increase with increasing temperature (Michaelis and Menten, 1913). This finding becomes apparent in the observed Gaussian relationship between NNM rates in 0–10 cm soil depth, mean WFPS and mean temperature in −5 cm soil depth during the incubation period (Fig. 4). Significant effects of soil moisture and temperature on NNM or nitrification rates where also reported by other studies (e.g. Kowalenko and Cameron, 1976; Goodroad and Keeney, 1984; Gonçalves and Carlyle, 1994). The observed minor reduction in N turnover with increasing soil depth furthermore reflects the influence of temperature and aeration on mineralization processes. We attributed the significantly lower NNM rates at the undrained site to limitation of micro-organisms by anaerobicity due to the permanently high water levels. The oxygen deficit at the undrained site also explained that NNM was solely determined by net ammonification. Events of NO_3^- presence and NO_3^- consumption in the upper soil layer suggest that in periods of low water level net nitrification also occurs at the undrained site. In contrast, at the well aerated drained sites, produced NH_4^+ becomes immediately oxidized to NO_3^-, hence net nitrification entirely controls the NNM. However, using NNM rates as indicator for soil N dynamics bears the risk to considerably underestimate the intensity and complexity of the real N

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fluxes (Augustin, 2003), thus further investigations should rather use the ^{15}N isotope dilution method (e.g. Davidson et al., 1991) for measuring gross rates of all relevant N turnover processes.

The detected permanently high mineral N contents in the probed soil depth probably indicate that the investigated alder forest has reached N saturation, due to the fact that the availability of N exceeds the biotic uptake capacity of the system (Aber et al., 1989). High contents of available NO_3^- in the soil carry the risk of leaching or gaseous losses (Robertson, 1982). Several studies reported NO_3^- losses by leaching from soils under alder stands (e.g. Binkley et al., 1992; Van Miegroet et al., 1992; Compton et al., 2003; Uri et al., 2011). The slightly higher NO_3^- contents but observed lower NNM rates in the soil depth 10–20 cm compared to the soil depth 0–10 cm at the drained sites probably indicate leaching of NO_3^- into deeper soil layers. Analysis of groundwater samples from the investigated sites showed nitrate contents of up to 36.2 mg L^{-1} and dissolved organic nitrogen (DON) contents of up to 2.8 mg L^{-1} (Tiemeyer personal communication), confirming the earlier assumption of N leaching. Nitrate leaching into the anaerobic peat profile can result in enhanced denitrification (Regina et al., 1996), wherein the ratio of N_2O/N_2 depends on the residence time of N_2O during its way from the production site in the anaerobic subsoil to the atmosphere (van Groenigen et al., 2005).

4.2 Factors controlling temporal and site-specific variation in N_2O and N_2 fluxes

In the present study, observed field N_2O fluxes at the drained sites are very low. Different studies reported considerably higher values for N_2O emissions from drained black alder stands, varying from 5–75 kg N ha^{-1} yr^{-1} (Mogge et al., 1998; Augustin, 1998; Brumme et al., 1999; Merbach et al., 2001; Hefting et al., 2003; von Arnold et al., 2005). According to Klemedtsson et al. (2005) NO_3^- availability is the main driver of N_2O emissions from drained histosols. However, despite distinct differences in the NO_3^- contents and NNM rates, significantly different N_2O emissions between the three sites

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were not found in the present study. This was in contrast to our hypothesis that accelerated N turnover and N mineralization leads to significantly increased amounts of N_2O emissions. We cannot rule out, however, that we may have missed high N_2O events on the drained sites due to our regular measurement intervals. In addition many wetland adapted trees such as alder can mediate N_2O fluxes from the soil to the atmosphere through the stem (Rusch and Rennenberg, 1998; Machacova et al., 2012; Pangala et al., 2012). This flux was not taken into account in the present study so that this study may underestimate the N_2O emissions from the alder ecosystem.

In the investigated alder forest, temperature in −2 cm soil depth and the GW level best explained field N_2O flux rates, whereas no relationship was found between field N_2O fluxes and the amount of NO_3^- in the soil. It is well known that temperature is a key variable affecting the emission rates of N_2O because both nitrification and denitrification are microbial processes (Firestone and Davidson, 1989; Maag and Vinther, 1996; Smith et al., 1998; Dobbie and Smith, 2001). Higher soil moisture content increases N_2O emissions through higher denitrification rates (Wolf and Russow, 2000). In our study, however, temperature and moisture only explained 37 % of the spatio-temporal variation of mean N_2O flux rates. This demonstrates the complex interlinkage of the controlling factors for N_2O emissions, as reported for agricultural soils by Jungkunst et al. (2006). The observed cubic response to the GW level in our N_2O model reveals maximum N_2O emissions at a certain GW level. This was in line with investigations from Jungkunst et al. (2004) who found highest N_2O emissions at a GW level of −20 cm, whereas higher or lower GW levels decreased the emissions. Therefore we assume that a mean GW level between those measured at the observed sites D-1 and U would result in enhanced N_2O emissions at the present black alder forest. Indeed, Brumme et al. (1999) reported that small seasonal fluctuations of the GW level seem to be more important than the mean GW level.

In the laboratory experiment, however, significantly different N_2O emissions were not observed between the two adjusted soil moisture contents. But total denitrification was considerably higher at 100 % WFPS compared to 70 % WFPS for both sites. The

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proportion of N_2O emissions at 100 % WFPS amounted to ~ 1 to 6 % and to ~ 0.7 to 2 % of total N release from denitrification for samples from site D-2 and U, indicating that losses of N_2O are only of minor importance compared to N_2 losses at water saturated conditions. This agrees with findings that with increasing anoxic conditions the percentage of N_2 increases until it becomes the major gas evolved (Rolston et al., 1978; Davidson, 1991). N_2O fluxes only declined in D-2 samples at water saturated conditions and 25 °C with simultaneously exponentially increasing N_2 fluxes. While this mechanism supports our hypothesis that N_2O release is displaced by N_2 losses during periods of temporarily high water levels, the field observations never reached the point in which decreasing $N_2O : N_2$ ratio overcompensated the increasing denitrification rate.

In contrast to the field observations significant differences in the N_2O fluxes between the two investigated sites were found in the conducted incubation experiment at both soil moisture contents, mainly due to the distinct differences in the N_2O reaction to temperature. Obviously, denitrification was limited by temperate in the drained site, but limited by other factors in the undrained site, like the availability of labile organic carbon, available NO_3^-, or soil moisture (Letey et al., 1980; Knowles, 1982; Weier et al., 1993; Klemedtsson et al., 2005). We can rule out that redox conditions or microbial activity were less favorable for denitrification in samples from the undrained site in the incubation experiment because no CH_4 emissions were detected from water saturated soil cores and aerobic and anaerobic CO_2 production were comparable and showed a distinct temperature response at both sites. Thus we attribute the small temperature response of N_2O and denitrification of the undrained site to NO_3^- limitation. The amount of NO_3^- in the solution from soil cores was not ascertained, but in the field net nitrification could never be detected at the undrained site. However, temporarily measured N_2O fluxes confirm our assumption that in periods of low water level also net nitrification occurs at the undrained site, albeit at a low level. Thus, we conclude that most of the year denitrification activity is NO_3^- limited at the undrained site, confirming our hypothesis that NO_3^- limitation in permanently waterlogged peat soils results in negligible N_2O and N_2 losses.

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For N_2 fluxes no comparable values from the field are available in the literature but observed N_2 fluxes in the incubation experiment are in the range of other studies from drained and undrained fen ecosystems (e.g. Teiter and Mander, 2005; Wray and Bayley, 2007; Mander et al., 2008; Roobroeck et al., 2010; Soosaar et al., 2011).

In the present study less than 0.2 % of the nitrified N was emitted as N_2O-N at the drained sites. Similar or slightly higher values were reported by Klemedtsson et al. (1988) and Maag and Vinther (1996). Up to four times higher N_2O fluxes were measured in the incubation experiment at samples for site D-2 compared to the field fluxes. This indicates the potential of high N_2O emissions from the drained alder sites under different soil physical conditions.

The low N_2O and N_2 losses, despite very high N mineralization rates perhaps indicate that most of the year, aerobic or only slightly anaerobic soil conditions are predominant at the drained sites. Thus, a certain proportion of the gaseous N may have been lost as nitric oxide (NO), a by-product of nitrification and an intermediate product of denitrification (Davidson, 1991). Several studies reported that net nitrification rates and NO_3^- in the soil solution are positively correlated to NO fluxes in well-aerated soils (Skiba et al., 1998; Gasche and Papen, 1999; Skiba et al., 1999; Venterea et al., 2003; Eickenscheidt and Brumme, 2012).

5 Conclusions

We studied N turnover processes in organic soils along a water table gradient in a nitrogen-saturated alder forest characterized by high mineral N concentrations. Drainage considerably increased net N mineralization and N turnover processes and shifted the dominant process from net ammonification to net nitrification, resulting in nitrate leaching. Surprisingly, N_2O emissions in the field remained low at the drained sites, but we cannot rule out that we have missed N_2O emission peaks. The incubation experiment supported the potential for high N_2O emissions at the drained alder sites. Temporally water-saturated conditions enhanced N_2 emissions, whereas N_2O emis-

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sions remained unchanged. In contrast, the permanently high groundwater level at the undrained site prevented net nitrification and resulted in negligible gaseous N losses.

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Table 1. Groundwater level, water filled pore space (WFPS), extractable nitrate (NO_3^-) and ammonium (NH_4^+) contents of the three sites for the year 2011.

	Soil depth [cm]	U	D-1	D-2	*n*
Groundwater level [cm]		4 (−26/28)[1] 3 (−20/22)[2]	−41 (−71/−3) −42 (−65/−22)	−47 (−77/−5) −44 (−68/−25)	81
WFPS [Vol %]	0–10	97 (79/100) a	70 (56/87) b	63 (51/73) c	26
	10–20	99 (92/100) a	81 (65/95) b	78 (66/88) c	26
NO_3^- [mg N kg^{-1}]	0–10	7 (0/57) a	103 (36/196) b	60 (24/106) c	26
	10–20	4 (0/21) a	109 (55/193) b	62 (28/109) c	26
NH_4^+ [mg N kg^{-1}]	0–10	73 (0/209) a	18 (0/88) b	10 (0/58) b	26
	10–20	68 (0/169) a	11 (0/57) b	6 (0/24) b	26

Values are given as mean with minimum and maximum in parentheses. Means followed by the same lower-case letters indicate no significant differences among the sites within the year 2011. (Pairwise Wilcoxon Rank sum test with Bonferroni correction for WFPS, NO_3^- and NH_4^+ at $P \leq 0.05$).

[1] Values present mean data from the water level loggers (15 min log interval).

[2] Values present the mean groundwater level during the conducted gas flux measurements.

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Table 2. Soil properties of the sites.

	Soil depth	U	D-1	D-2	*n*
Soil type (WRB* 2006)		Fluvisol	Sapric Histosol	Sapric Histosol	
Soil type (German classification KA5)		DY	KV-KM	KV-KM	
Peat depth [cm]		60	90	90	1
Organic carbon [%]	0–10 cm	35.2 ± 1.4	14.6 ± 0.1	9.7 ± 0.4	3
	10–20 cm	30.2 ± 0.6	13 ± 0.1	8.3 ± 0.2	3
Total nitrogen [%]	0–10 cm	2.8 ± 0.1	1.8 ± 0.1	1.1 ± 0.0	3
	10–20 cm	2.0 ± 0.0	1.5 ± 0.1	0.9 ± 0.0	3
C/N ratio	0–10 cm	13 ± 0	11 ± 0	13 ± 1	3
	10–20 cm	16 ± 0	12 ± 1	14 ± 0	3
Bulk density [g cm^{-3}]	0–10 cm	0.14 ± 0.01	0.36 ± 0.02	0.47 ± 0.04	6
	10–20 cm	0.13 ± 0.00	0.43 ± 0.01	0.60 ± 0.03	6
Porosity [%]	0–10 cm	89 ± 3	79 ± 2	74 ± 1	6
	10–20 cm	92 ± 1	79 ± 1	75 ± 1	6

Values present means ± standard error.
* World Reference Base for Soil Resources

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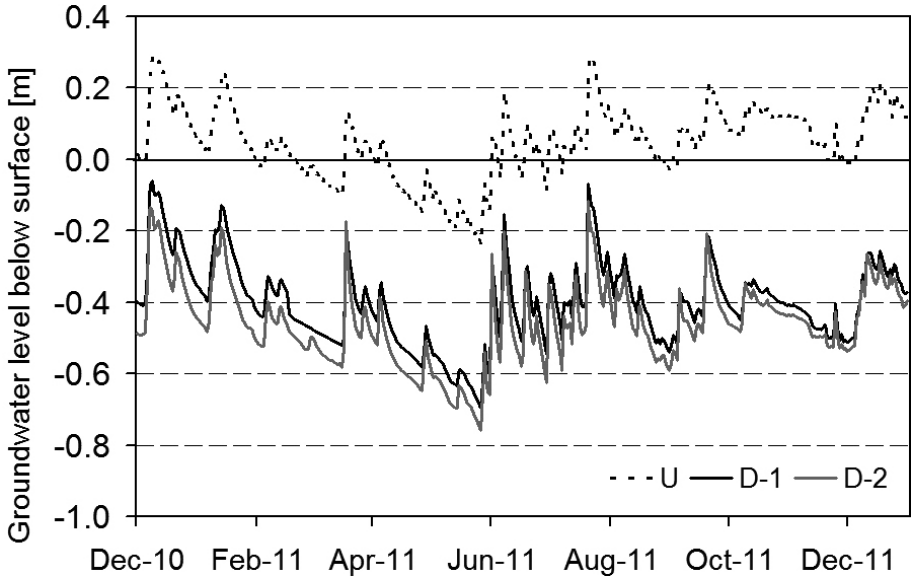

Fig. 1. Annual variation in the groundwater level (U = undrained, D-1 = drained site 1, D-2 = drained site 2).

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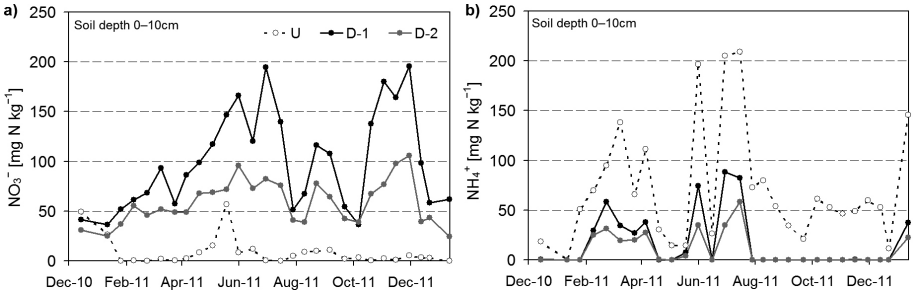

Fig. 2. Annual variation in the extractable NO_3^- **(a)** and NH_4^+ **(b)** contents for the soil depth 0–10 cm (U = undrained, D-1 = drained site 1, D-2 = drained site 2).

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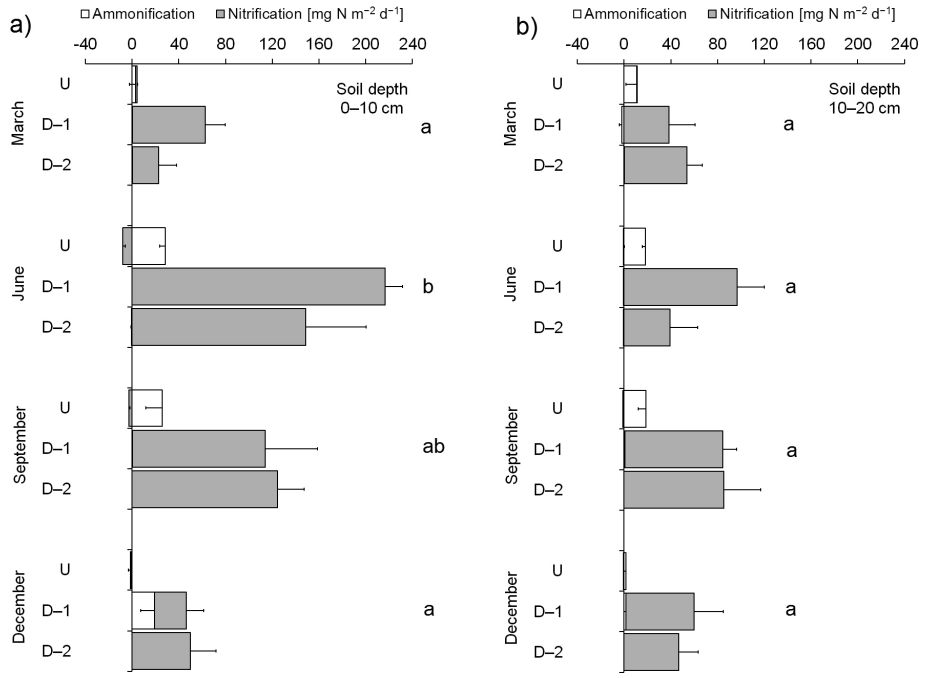

Fig. 3. Net ammonification, net nitrification and net N mineralization rates (sum of net ammonification and net nitrification rate) for the soil depth 0–10 cm **(a)** and 10–20 cm **(b)**. Means (± SE; $n = 3$) followed by the same letter indicated no significant differences in the net N mineralization rate among the months within one soil depth (Two-way ANOVA, Tukey-HSD-test at $P \leq 0.05$). Differences among both soil depths are not significant.

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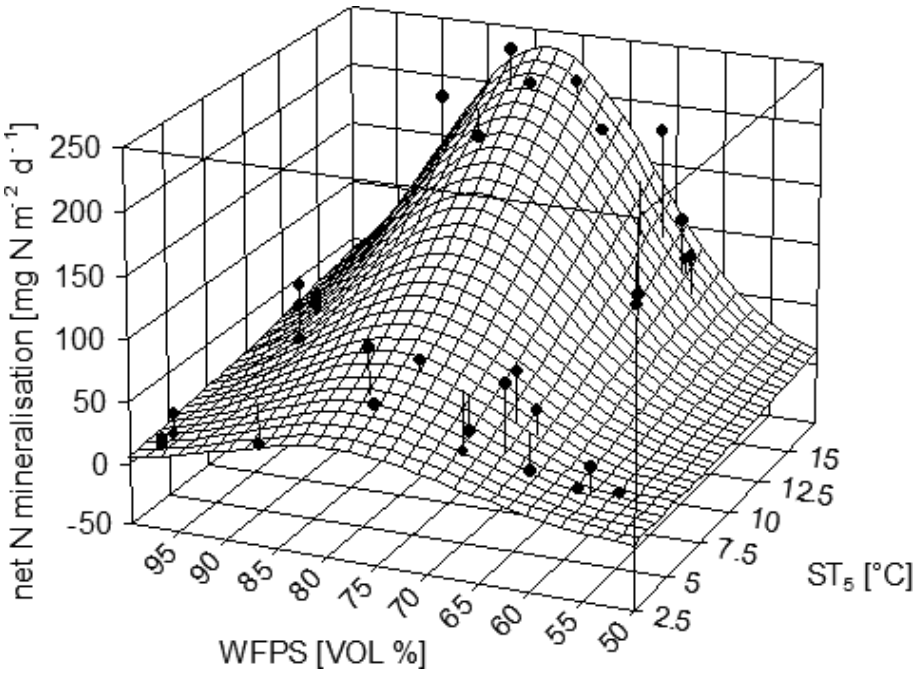

Fig. 4. Relationship of net N mineralization in 0–10 cm soil depth (y) to mean water filled pore space (x 1) and mean soil temperature in 5 cm soil depth (x 2) over 21 days of in situ incubation. Equation formula is $y = 304.28(\pm 85.27)\cdot\exp(-0.5\cdot((((\mathrm{WFPS} - 25.72(\pm 4.46))/11.47(\pm 1.14))^2) + (((\mathrm{ST}_5 - 78.60(\pm 1.15))/11.47(\pm 1.14))^2)))$. ($n = 36$; adj $-R^2 = 0.75$; $P < 0.0001$).

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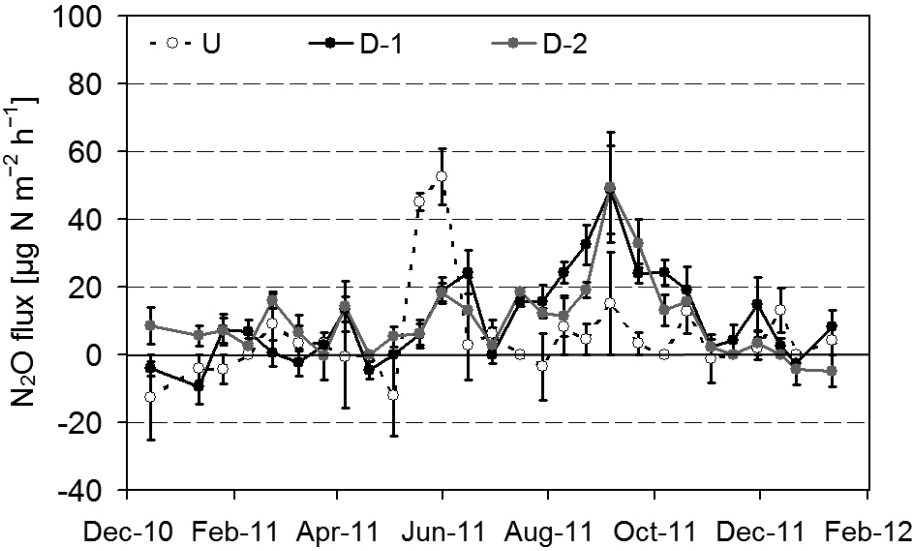

Fig. 5. Mean (±SE, $n = 3$) N_2 O fluxes of the undrained (U), drained 1 (D-1) and drained 2 (D-2) sites.

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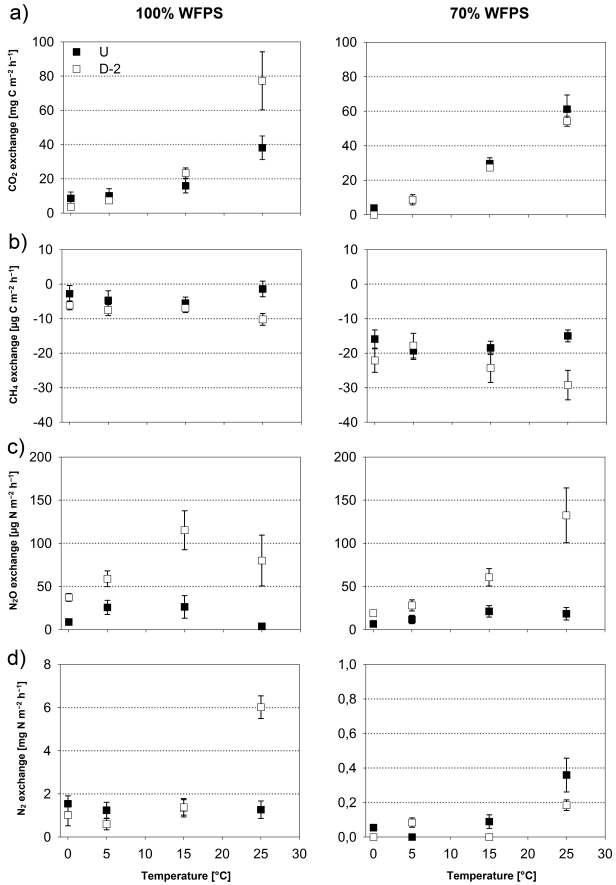

Fig. 6. Mean (±SE, $n = 5$) of CO_2 **(a)**, CH_4 **(b)**, N_2O **(c)** and N_2 **(d)** exchange rates per water filled pore space (Vol. %), temperature (°C) and site treatment. U = undrained, D-2 = drained 2. Please note the different scales for the N_2 exchange rates.

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