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Nutrient and carbon dynamics in peat from rich fens and *Sphagnum*-fens during different gradations of drought

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ABSTRACT

Drought has major impacts on microbial decomposition and net N- and P-release in peat. The separate effects of aeration (oxygen intrusion) during moderate drought and desiccation (oxygen intrusion plus water deficiency) during severe drought are, however, poorly understood. This information is vital to understand the biogeochemical and ecological effects of different gradations of drought in peatlands. In addition, effects may differ between rich fen peat and *Sphagnum*-dominated poor fen peat. We therefore conducted a controlled incubation experiment involving both soil types to quantify the rates of decomposition, net N-mineralization, net P-release, denitrification, and the partitioning of C, N and P in soils and microbial biomass under three different incubation conditions. Soils were incubated under (1) anaerobic, waterlogged conditions, (2) aerobic, moist conditions, characteristic for moderate drought in which oxygen intrusion takes place, and (3) aerobic, desiccated conditions to simulate severe drought.

Our results show that under anaerobic, waterlogged conditions, net N-mineralization rates per mass dry peat soil and per microbial C mass were much higher (on average 10 times) in the *Sphagnum*-peat than in peat from rich fens, probably caused by higher microbial N-demand and N-immobilization in rich fens. The response upon aeration differed greatly between rich fen peat and *Sphagnum*-peat. Whereas aeration led to increased carbon loss and net N-mineralization rates in the rich fen peat, these rates did not change for *Sphagnum*-peat. The absence of aeration effects in *Sphagnum*-dominated fens suggests that decomposition rates are more strongly determined by litter quality than by oxygen intrusion. Upon further desiccation, both net P-release and DOC production, which remained unchanged upon aeration, increased significantly in both fen types. This may be due to microbial mortality and/or a change in microbial composition. The low anaerobic net N-mineralization rates and the strong response to aeration in rich fens compared to *Sphagnum*-fens, as well as the strong increase in P-availability upon further desiccation in both fen types, have important implications for peatland management in relation to drought.

1. Introduction

Acidification and eutrophication are considered a threat to nitrogen- and phosphorus-limited, minerotrophic base-rich fens, which are generally called 'rich fens' (Kooijman, 1992, 2012; Van Wirdum, 1993; Paulissen et al., 2004). These rich fens belong to the EU priority habitat H7140; Transition mires and quacking bogs. For the conservation of rich fens, it is important to keep these habitats base-rich, and nutrient-poor. As the water level is a key factor determining the biogeochemical processes and functioning of wetlands (Reddy and Patrick, 1974; Loeb et al., 2008) and wetland hydrology in densely populated regions across the world has strongly been affected by anthropogenic influence (Lamers et al., 2002; Limpens et al., 2008), it is important to gain insight into the biogeochemical processes resulting from water level drawdown with regard to net mobilization of nutrients in these fens.

As undisturbed wetlands are generally characterized by high water levels, the decomposition of organic matter is mainly carried out by microorganisms that require electron acceptors other than O_2 (McLatchey and Reddy, 1998). This leads to the

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sequential reduction of nitrate, iron and sulfate, and finally methanogenesis (Mitsch and Gosselink, 1993; Stumm and Morgan, 1996), which are relatively slow processes compared to aerobic decomposition. However, as many wetlands are affected by water level drawdown, the redox potential in the soil increases (see Appendix A, Supplementary data), and aerobic oxidation processes may prevail. This may lead to acidification as a result of the use of oxygen (Stumm and Morgan, 1996) and, if more severe, to limitations as a result of water shortage. These radical biogeochemical changes are expected to affect the availability of nutrients, especially in peatlands where microbial mineralization of organic N and P is the main source of nutrients (Verhoeven, 1986; Verhoeven et al., 1988). Although it has been generally assumed that lowering of the water level in fens results in increased microbial decomposition and thus increased mineralization of nutrients (Williams and Wheatley, 1988; Bridgham et al., 1998; Updegraff et al., 1995; Olde Venterink et al., 2002; Holden et al., 2004), the relationships between aeration and desiccation of peat soils and the actual net release of N and P are poorly understood (Olde Venterink et al., 2002).

Decomposition and mineralization may also be affected by the acid neutralizing capacity (ANC) of a peatland (Verhoeven et al., 1988, 1990; Kooijman and Hedenäs, 2009). It has been generally assumed that in mineral-rich wetlands the conditions for litter decay and nutrient turnover are more favorable than in mineral-poor wetlands, leading to higher net N-mineralization rates and increased nutrient availability for plants in rich fens as compared to ombrotrophic *Sphagnum*-fens (Bayley et al., 2005). However, high decomposition rates do not by definition lead to high net N- and P-mineralization rates (Kooijman et al., 2008; Kooijman and Hedenäs, 2009). In addition, net N- and P-mineralization do not necessarily increase with pH, and often increase from rich fens to poor fens (Verhoeven et al., 1988, 1990; Bridgham et al., 1998; Scheffer et al., 2001; Kooijman and Hedenäs, 2009). Additional experimental research is therefore needed to assess whether the ANC in fens also affects the changes induced by aeration and desiccation. Although oxygen deficiency is considered a major factor limiting microbial decomposition rates, these rates may also be strongly limited by litter quality and enzyme activity (Freeman et al., 2004) in poor, *Sphagnum*-dominated fens, which may interact with drought effects.

The main objective of this study was to gain insight into the effects of aeration (increased oxygen intrusion) and desiccation (oxygen intrusion plus water shortage) on decomposition rates and net release rates of nutrients upon water level drawdown in fens, and to investigate whether these responses are affected by ANC of the peat. Therefore, we conducted a laboratory incubation experiment involving soils from both rich fens and *Sphagnum*-dominated fens. Microbial processes were studied under (1) anaerobic, moist conditions, (2) aerobic, moist conditions, which are characteristic for moderate drought in which oxygen intrusion takes place, and (3) aerobic, desiccated conditions, characteristic for severe drought. We expected lowering of the pH and an increase of microbial decomposition rates and net nutrient mineralization rates upon drought. We also hypothesized that the net release rates of nutrients differ between rich fens and *Sphagnum*-fens due to differences in microbial immobilization characteristics. The following responses are discussed in this paper: (1) acidification as a result of oxygen intrusion, (2) changes in carbon (C) mineralization, (3) changes in net N-mineralization, and (4) changes in net P-release. In addition, implications for the hydrological management of both rich fens and *Sphagnum*-dominated fens are discussed.

2. Material and methods

2.1. Sampling

Peat soil samples were collected from three locations in the Netherlands (Fig. 1): Stobbenribben (ST), Kiersche Wiede (KW) and Binnenpolder Tienhoven (BPT). Stobbenribben and Kiersche Wiede are situated in the northwestern part of the province of Overijssel and are part of the extensive Ramsar fen area Wieden-Weerribben, in which most of the peat soils remain relatively base-rich due to the supply of lithotrophic surface water (Van Wirdum, 1991). Binnenpolder Tienhoven is part of the Vechtplassen area, which is characterized by the discharge of base-rich groundwater in the river plain of the river Vecht (Schot, 1991). All locations also show sub-locations with lower ANC, characterized by *Sphagnum* dominance.

Peat samples were collected in November 2011 and kept at field moisture content. From each of the three locations, five samples were collected from a mineral-rich, brown moss-dominated site, and five from an ombrotrophic, *Sphagnum*-dominated site ($n = 30$). Rich fen sites were characterized by the bryophytes *Scorpidium scorpioides* (Hedw.) Limpr. and *Hamatocaulis vernicosus* (Mitt.) Hedenäs. Bryophytes are good indicators of environmental conditions in the top layer, because they have no roots and remain in direct contact with the surrounding water through one cell layer thick leaves without cuticula (Proctor, 1982). *Sphagnum palustre* (L.), unable to survive in calcareous water (Clymo and Hayward, 1982), indicates relatively ombrotrophic conditions.

In Stobbenribben and Binnenpolder Tienhoven, rich fen samples were collected from sites dominated by *S. scorpioides*, and in the Kiersche Wiede from *H. vernicosus*-dominated sites. All *Sphagnum*-dominated samples were collected from sites dominated by *S. palustre*, which were situated within 25 m from the rich fen sites.

Fig. 1. The three different research areas in the Netherlands: Stobbenribben (N 52°47′5.5″, E 5°59′1″), Kiersche Wiede (52°41′47.8″, E 6°7′57″) and Binnenpolder Tienhoven (N 52°10′30.7″, E 5°6′0.4″).

Samples were collected from the upper 10 cm of the peat soil, just below the living moss layer. Samples for bulk density were collected by using a steel corer with an exact volume of 100 ml. All samples were collected in plastic bags to avoid oxygen exposure, and stored at 4 °C.

2.2. Experimental setup and chemical analyses

Three different conditions were simulated during incubation: (1) anaerobic (moist) incubation for 69 days, (2) aerobic (moist) incubation for 62 days and (3) aerobic (dry) incubation for 90 days. For logistical reasons, incubation periods differed, but the results have been corrected for these differences in incubation time. For all treatments, fresh samples were homogenized by hand, placed into petri dishes with a diameter of 15 cm, and stored in the dark at 20 °C. Rich fen and *Sphagnum* samples were incubated under field-moist conditions with a gravimetric moisture content of respectively 15 and 25 g water per g dry peat soil. To simulate permanently wet and anaerobic conditions, fresh soil samples were placed in a glove box (Plas-Labs Inc., 855 Series), filled with inert argon gas 5.0. For aerobic incubation, samples were placed under ambient air conditions. All anaerobic and moist aerobic samples were kept at field moisture by weekly adding demineralized water, based on the initial weight of the samples. For the dry, aerobic situation, samples were dried out gradually to air-dry conditions.

Before starting the incubation, initial soil characteristics of the soil samples were measured. Total C and N contents of dry peat soil were measured using a CHNS analyzer (Elementar, Vario EL Cube). Furthermore, portions of 250 mg dry peat soil were digested for 50 min in a microwave (Perkin–Elmer, Multiwave) with 4.0 ml HNO_3 (65%) and 1.0 ml HCl (37%), after which total P, Fe, Ca, Mg and S contents were measured by ICP (Perkin–Elmer, Optima 3000XL) (Bettinelli et al., 1989; Westerman, 1990).

Rates of CO_2 production (soil respiration), CH_4 uptake/production and N_2 emission were measured at the beginning and at the end of the incubation period in 100 ml serum bottles containing 7–10 g of peat soil. For the anaerobic samples, these serum bottles were filled inside the glove box to maintain anaerobic conditions. Rates of N_2 emission were only measured for anaerobic incubation, and rates of CH_4 emission or consumption (of ambient CH_4) were only measured for anaerobic and moist aerobic incubation. Over a period of two days, four measurements were carried out for each sample. Concentrations were measured by chromatography using Varian 3600 GC for CO_2 and CH_4, and Shimadzu GC-8A for N_2, with helium as carrier gas. Concentrations were determined by calibration relative to standard gas, and production rates were calculated from the differences in headspace concentrations in the serum bottles over time. Initial headspace concentrations were similar to ambient concentrations. Total denitrification rates may have been underestimated since only fluxes of N_2 were measured, and fluxes of N_2O were not taken into account.

Before and after incubation pH values of the soil samples were determined in water extracts. After 2 h of shaking, pH was measured with a Consort C831 pH meter, using a solid(g):liquid(g) ratio of 1:10. Also gravimetric moisture content, expressed as a percentage of the sample's dry weight, was determined for all fresh samples before incubation and for the samples that were incubated under dry aerobic conditions, by drying the soil samples for 24 h at 105 °C.

Concentrations of extractable inorganic N (NH_4 and NO_3), orthophosphate (PO_4), and dissolved organic carbon (DOC) in both fresh and incubated samples were determined via extraction with 50 ml 0.05 M K_2SO_4 solution (Westerman, 1990). A solid(-g):liquid(g) ratio of 1:50 was used for the rich fen samples and 1:80 for the *Sphagnum*-fens, because the *Sphagnum*-peat absorbs much solution. After 1 h of shaking in 100 ml bottles, extraction solutions were collected by using Rhizon SMS soil moisture samplers (Rhizon SMS-10 cm; Eijkelkamp Agrisearch Equipment, the Netherlands), which were connected to vacuum serum bottles. Concentrations were measured by using an Auto Analyzer (Skalar, San^{++} System, fitted with Skalar, SA1074). Rates of net N-mineralization and net P-release were calculated as the difference in total extractable inorganic N (NH_4 and NO_3) and P (PO_4) concentrations between initial samples and incubated samples.

Microbial C and N were determined by chloroform fumigation extraction (Jenkinson and Powlson, 1976; Brookes et al., 1985; Vance et al., 1987). Before and after incubation, samples were flushed with chloroform for 24 h. Microbial C and N were determined by measuring total extractable DON (dissolved organic nitrogen), DOC and inorganic N (NH_4 and NO_3) concentrations in 0.05 M K_2SO_4 extractions, as described in the previous paragraph. The differences between fumigated and non-fumigated samples were used to calculate the microbial C and N content, assuming an extractability of 0.45 (Jenkinson and Ladd, 1981; Wu et al., 1990).

2.3. Calculations of gross N-mineralization and microbial N-immobilization

In order to explain differences in net N-mineralization between treatments, several aspects of microbial growth and nutrient efficiency were calculated (Table 1). The equations were adapted after Kooijman et al. (2008), in which C and N dynamics were described based on existing theoretical models (Berendse et al., 1989; Tietema and Wessel, 1992). Measured values for the CO_2 emission (Q), net N-mineralization rates (NM), denitrification rates (D), N:C ratios of the peat substrate (NC_s), and averaged microbial N:C ratios during the incubation period (NC_m) were used to estimate the microbial growth efficiency (eC), which is the fraction of gross C-release that is used for microbial assimilation. In addition, gross N-release rates (GN), N-immobilization rates (*I*) and the microbial N-immobilization efficiencies (eN) were estimated. We, however, emphasize that this is only a clarifying approach to get insight into the microbial processes that are important, and by no means a complete model. The model was not applied to explain microbial characteristics concerning P, since the net P-release is not only associated with microbial net P-mineralization, but also to a high extent dependent on redox-sensitive chemical binding of P.

Table 1
List of symbols and used equations (derived and reformulated from Kooijman et al., 2008).

Measured variables		Unit
NM	Net N-mineralization	μmol N kg^{-1} d^{-1}
Q	Respiration (CO_2 emission)	μmol C kg^{-1} d^{-1}
NC_m	N:C-ratio in microbial biomass	mol N/mol C
NC_s	N:C-ratio in peat substrate	mol N/mol C
D	Denitrification	μmol N kg^{-1} d^{-1}
Calculated variables		
eC	Microbial growth efficiency	mol C/mol C
GN	Gross N-release	μmol N kg^{-1} d^{-1}
I	N-immobilization	μmol N kg^{-1} d^{-1}
eN	Microbial N-immobilization efficiency	mol N/mol C
Equations used		
1	$NM = GN - I - D$	
2	$NM = ((NC_s{*}Q)/(1 - eC)) - ((eC{*}NC_m{*}Q)/(1 - eC)) - D$	
3	$eC = ((NC_s{*}Q) - (NM + D))/((NC_m{*}Q) - (NM + D))$	
4	$GN = (1/(1 - eC)){*}NC_s{*}Q$	
5	$I = (eC/(1 - eC)){*}NC_m{*}Q$	
6	$eN = eC{*}(NC_m/NC_s)$	

2.4. Statistical analysis

All statistical analyses were performed using SPSS 20.0 for Windows (IBM Inc., 2011). Significance was accepted at a confidence level of $P < 0.05$. Initial differences in soil characteristics between rich fens and *Sphagnum*-fens were tested by applying a two-way ANOVA, using fen type and location as two independent variables (i.e. fixed factors). We distinguished between fens with minerotrophic species (*S. scorpioides* and *H. vernicosus*) and fens with ombrotrophic species (*S. palustre*). Potential differences resulting from treatment conditions were tested by three-way ANOVA with LSD (least significant difference) post hoc analyses, using fen type, treatment, and location as three independent variables (i.e. fixed factors).

3. Results

3.1. Initial soil- and microbial characteristics

The initial soil characteristics before incubation clearly differed between both fen types for many variables (Table 2). As expected, pH values were considerably higher in rich fens than in *Sphagnum*-fens ($F_{1,24} = 2893.0$; $P < 0.001$). The effect of location on pH was the strongest for rich fens, considering a significant interaction effect of location*fen type ($F_{2,24} = 217.3$; $P < 0.001$). In the KW rich fen, initial pH was lower than in the other rich fens. Total N and P concentrations in rich fen peat were, on average, 1.8 times as high as in *Sphagnum*-fens, resulting in lower C:N ratios ($F_{1,12} = 10764.0$; $P < 0.001$) and C:P ratios ($F_{1,12} = 504.1$; $P < 0.001$) in rich fen peat. Total P concentrations were the lowest in the ST, resulting in significantly higher C:P ratios ($F_{2,12} = 314.5$; $P < 0.001$) and N:P ratios ($F_{2,12} = 315.3$; $P < 0.001$). The rich fen soils were also characterized by higher total concentrations of Ca ($F_{1,12} = 886.3$; $P < 0.001$), although this was largely due to the ST site where Ca concentrations were 10 times higher for rich fen than for poor fen, as indicated by a significant interaction effect of location*fen type ($F_{2,12} = 595.2$; $P < 0.001$). Fe concentrations were also higher in rich fen peat ($F_{1,12} = 655.3$; $P < 0.001$), which was mainly due to the BPT rich fen where total Fe concentrations were about 10 times higher than in the other rich fens, as indicated by a significant interaction effect of location*fen type ($F_{2,12} = 1536.9$; $P < 0.001$). The effect of location on concentrations of extractable NH_4 was significant ($F_{2,24} = 148.2$; $P < 0.001$), and this effect was the strongest for rich fens, considering a significant interaction effect of location*fen type ($F_{2,24} = 26.3$; $P < 0.001$). Also extractable NO_3 concentrations differed between locations ($F_{2,24} = 117.8$; $P < 0.001$) and the effect of location was the strongest for rich fens, considering a significant interaction effect of location*fen type ($F_{2,24} = 93.1$; $P < 0.001$). Both extractable NH_4 and NO_3 concentrations were higher in the ST rich fen than in the other rich fens. Extractable PO_4 concentrations did not significantly differ between locations ($F_{2,24} = 2.5$; $P = 0.105$). In addition, bulk density was 2–3 times higher in rich fens ($F_{1,11} = 175.1$; $P < 0.001$), while gravimetric soil moisture content was twice as high in *Sphagnum*-dominated fens ($F_{1,24} = 128.2$; $P < 0.001$).

Anaerobic CO_2 production per kg dry peat soil at $T = 0$ did not differ significantly between both fen types ($F_{1,24} = 3.0$; $P = 0.098$) or between locations ($F_{2,24} = 0.2$; $P = 0.859$) (Table 2). However, if expressed per volume fresh peat soil, anaerobic CO_2 production rates at $T = 0$ in rich fens were significantly higher (factor 2.0 on average) than in *Sphagnum*-dominated fens ($F_{1,24} = 89.4$; $P < 0.001$), due to the lower bulk density of *Sphagnum*-peat. When expressed per mass of microbial C, respiration was higher (factor 1.7 on average) in the *Sphagnum*-fens ($F_{1,24} = 64.0$; $P < 0.001$), as the total concentration of microbial C was higher in rich fen peat ($F_{1,23} = 42.3$; $P < 0.001$). Anaerobic CH_4 fluxes per kg dry peat soil at $T = 0$ were negative for all samples, indicating microbial oxidation of CH_4. The anaerobic oxidation of CH_4 was, on average, two times higher in *Sphagnum*-fens than in rich fens ($F_{1,24} = 86.1$; $P < 0.001$). In addition, the overall concentration of microbial C in the KW location was significantly higher than in the other locations.

3.2. Treatment effects

3.2.1. Acidification

All outcomes of statistical analyses of the incubation results are shown in Table 3. Treatments had a significant effect on $[H^+]$. Both aeration and desiccation led to a net increase of $[H^+]$, hence to

Table 2
Initial characteristics of the peat soil and microbial biomass at $T = 0$ at the different research sites. Data shown represent mean values and their standard deviations ($n = 5$). * = significant difference ($P < 0.05$) between rich fen peat and *Sphagnum*-peat, † = significant difference ($P < 0.05$) between locations. ST = Stobbenribben, KW = Kiersche Wiede, BPT = Binnenpolder Tienhoven, d.w. = dry weight of peat soil. Positive fluxes indicate release.

Fen type	Rich fen			*Sphagnum*-fen		
Location	ST	KW	BPT	ST	KW	BPT
Dominant moss species	*S. scorpioides*	*H. vernicosus*	*S. scorpioides*	*S. palustre*	*S. palustre*	*S. palustre*
pH-H_2O*†	6.9 (0.1)	5.7 (0.2)	6.3 (0.2)	3.8 (0.0)	4.4 (0.0)	4.4 (0.1)
C_{total} (g kg^{-1} d.w.)†	464.0 (1.6)	481.7 (0.7)	331.3 (6.0)	469.9 (4.0)	454.1 (2.1)	460.9 (1.7)
N_{total} (g kg^{-1} d.w.)*†	17.5 (0.3)	22.5 (0.3)	16.4 (0.2)	11.4 (0.2)	10.6 (0.1)	10.3 (0.1)
P_{total} (g kg^{-1} d.w.)*†	0.6 (0.0)	1.0 (0.0)	1.1 (0.1)	0.3 (0.0)	0.7 (0.0)	0.5 (0.1)
Ca_{total} (g kg^{-1} d.w.)*†	22.6 (0.7)	9.1 (0.1)	11.4 (0.5)	2.2 (0.1)	7.5 (0.3)	10.3 (1.0)
Fe_{total} (g kg^{-1} d.w.)*†	1.3 (0.0)	2.0 (0.0)	17.0 (0.7)	1.1 (0.0)	6.0 (0.2)	1.9 (0.2)
Total Ca:Fe (mol/mol)*†	23.9 (0.4)	6.2 (0.0)	0.9 (0.0)	2.9 (0.1)	1.7 (0.1)	7.4 (0.1)
Substrate C:N ratio (g g^{-1})*	26.5 (0.3)	21.4 (0.3)	20.2 (0.1)	41.3 (0.5)	42.7 (0.5)	44.9 (0.5)
Substrate C:P ratio (g g^{-1})*†	823.4 (21.7)	480.3 (13.7)	294.7 (21.4)	1451 (42.9)	651.9 (14.6)	902.3 (7.2)
Substrate N:P ratio (g g^{-1})†	31.1 (0.8)	22.4 (0.7)	14.6 (1.0)	35.1 (1.1)	15.3 (0.5)	20.1 (2.2)
ext-NH_4^+ (mg kg^{-1} d.w.)*†	117.4 (23.2)	18.3 (5.2)	3.8 (0.9)	53.6 (13.7)	15.6 (3.9)	5.6 (1.0)
ext-NO_3^- (mg kg^{-1} d.w.)*†	23.0 (4.5)	1.2 (0.4)	1.0 (0.6)	2.2 (1.3)	1.3 (0.4)	0.7 (0.4)
ext-PO_4^{3-} (mg kg^{-1} d.w.)	12.1 (3.1)	18.8 (5.4)	7.8 (1.3)	18.6 (2.3)	11.2 (2.2)	16.9 (3.9)
Bulk density (mg d.w. cm^{-3})*†	64.9 (6.1)	49.3(5.0)	81.2 (10.4)	25.4 (6.9)	26.3 (2.7)	25.3 (0.7)
Gravim. moisture content (%)*	982 (58)	1421 (75)	889 (156)	2404 (263)	1747 (438)	1910 (63)
Microbial C (mg g^{-1} d.w.)*†	6.6 (0.7)	9.9 (1.8)	3.8 (0.5)	3.4 (0.3)	5.1 (0.5)	3.8 (1.1)
Anaerobic CO_2 flux $T = 0$ (mg C kg^{-1} d.w. d^{-1})	316.1 (77.1)	344.3 (97.3)	359.1 (34.8)	424.3 (59.5)	370.4 (30.9)	350.4 (74.8)
Anaerobic CO_2 flux $T = 0$ (g C dm^{-3} d^{-1})*	20.5 (5.0)	17.0 (4.8)	27.5 (2.9)	11.3 (2.2)	10.2 (1.0)	9.1 (2.2)
Anaerobic CO_2 flux $T = 0$ (mg C g^{-1} C_m d^{-1})*	48.6 (12.4)	36.3 (14.6)	104.1 (39.1)	131.6 (22.2)	76.8 (14.2)	103.4 (43.4)
Anaerobic CH_4 flux $T = 0$ (mg C kg^{-1} d.w. d^{-1})*†	−0.9 (0.2)	−1.3 (0.2)	−0.2 (0.2)	−2.2 (0.1)	−1.7 (0.2)	−0.3 (0.2)

Table 3
Outcomes of statistical analyses of the effects of fen type, treatment, location and their interaction effects, as tested by three-way ANOVA with LSD post hoc analyses. *F*-ratios are shown with their level of significance: $^{*}P < 0.05$, $^{**}P \leq 0.01$. D.f. denominator = 72, except for CH_4 flux per kg d.w. (d.f. denominator = 48) and N_2 flux per kg d.w. (d.f. denominator = 24). Different letters indicate significant differences ($P < 0.05$) between treatments, n.s. = not significant, d.w. = dry weight of peat soil.

Dependent variable	Fen type (d.f. = 1)	Treatment (d.f. = 2)	Location (d.f. = 2)	Fen type × treatment (d.f. = 2)	Fen type × location (d.f. = 2)	Treatment × location (d.f. = 4)	Anaerobic (moist)	Aerobic (moist)	Aerobic (dry)
Net d[H^+]	22.0**	7.9**	10.3**	3.2*	2.1	3.1*	a	b	b
d(pH)	136.4**	25.1**	8.7**	14.6**	0.5	1.0	a	b	b
CO_2 flux (per kg d.w.)	13.7**	9.7**	39.1**	13.2**	15.5**	5.1*	a	b	b
CO_2 flux (per $C_{microbial}$)	49.1**	25.0**	34.5**	16.6**	7.2**	20.9**	a	a	b
CO_2 flux (per dm^3)	697.0**	15.9**	138.5**	17.8**	121.0**	5.3**	a	b	b
Microbial C (per kg d.w.)	282.9**	35.6**	21.4**	24.3**	3.4*	12.5**	b	c	a
CH_4 flux (per kg d.w.)	79.8**	3.1	40.0**	53.1**	1.4	50.1**	n.s.	n.s.	–
DOC production (per kg d.w.)	44.2**	96.0**	22.1**	0.9	38.3**	1.9	b	a	c
DOC production (per dm^3)	5.5*	82.1**	64.7**	13.7**	77.0**	8.6**	b	a	c
Net N-mineralization (per kg d.w.)	149.1**	33.4**	173.5**	62.9**	14.3**	21.4**	a	b	a
Net N-mineralization (per $C_{microbial}$)	267.7**	7.5**	126.6**	23.0**	42.4**	18.7**	a	b	a
Net N-mineralization (per dm^3)	13.2	45.1**	119.2**	65.2**	6.9**	20.8**	a	c	b
N_2 flux (per kg d.w.)	65.1**	–	105.8**	–	27.8**	–	–	–	–
Gross N-mineralization (per kg d.w.)	546.5**	13.7**	102.7**	13.2**	86.9**	6.4**	a	c	b
Gross N-mineralization (per $C_{microbial}$)	58.6**	33.5**	51.7**	26.4**	36.9**	23.4**	a	a	b
N-immobilization (per kg d.w.)	633.1**	8.6**	164.2**	3.1	70.3**	10.9**	a	b	b
N-immobilization (per $C_{microbial}$)	167.1**	44.5**	92.6**	16.9**	30.1**	19.9**	a	a	b
Net P-release (per kg d.w.)	0.7	351.4**	8.7**	0.8	14.3**	13.6**	b	a	c
Net P-release (per $C_{microbial}$)	3.4	341.7**	1.6	20.4**	10.2**	8.1**	b	a	c
Net P-release (per dm^3)	18.7**	255.9**	13.9**	44.8**	16.7**	19.2**	a	a	b

significant lowering of the pH (Fig. 2). Overall, the net increase of [H^+] during incubation was greater in *Sphagnum*-fens than in rich fens. However, the effect of aeration and desiccation on lowering of the pH was stronger in rich fens, as indicated by a significant interaction effect of fen type*treatment. In the ST location the effect of aeration and desiccation on pH was less strong than in the other locations.

3.2.2. Carbon cycling

During incubation, the overall effect of fen type and treatment on the CO_2 emission per kg dry peat soil were significant and considering a significant interaction effect of fen type*treatment, the effect of treatment was stronger for rich fens (Table 3). Both aeration and desiccation led to increased CO_2 emission when expressed per kg dry peat, but only in rich fens and not in *Sphagnum*-fens (Fig. 3). As the overall concentration of microbial C mass per kg dry peat was on average two times lower in *Sphagnum*-fens, overall CO_2 emission per mass unit microbial C was on average 1.5 times higher in *Sphagnum*-fens than in rich fens. Overall CO_2 emission expressed per volume peat soil was on average 3.0 times higher in rich fens than in *Sphagnum*-fens, due to the higher bulk density of rich fen peat. Also, DOC production per kg dry peat soil was significantly affected by treatment. DOC production showed a slight but significant decrease upon aeration, while desiccation resulted in a considerable increase of DOC concentrations. CH_4 fluxes expressed per kg dry peat became clearly positive under moist anaerobic conditions only in two rich fens (KW and BPT), while in all *Sphagnum*-fens CH_4 fluxes remained negative. CH_4 fluxes were negative for all fens upon aeration, and aeration seemed to have a leveling effect for both fen types.

3.2.3. Nitrogen cycling

Especially under anaerobic conditions, net N-mineralization rates per kg dry peat soil and per microbial C mass were much higher (on average 10 times) in the *Sphagnum*-fens than in the rich fens (Fig. 4, Table 3). Due to the high bulk density of rich fen peat compared to *Sphagnum*-peat, the differences in net N-mineralization when expressed per volume peat soil were smaller, but on average still 4 times higher in *Sphagnum*-peat than in rich fen peat. Anaerobic denitrification rates per kg dry peat soil were relatively high in the rich fens compared to the net N-mineralization rates (on average 91%) and relatively low in the *Sphagnum*-fens (on average 14%), and in absolute terms anaerobic denitrification rates were lower in rich fen peat than in *Sphagnum*-peat. In contrast to net N-mineralization, estimated gross N-mineralization was overall higher in rich fens than in *Sphagnum*-fens, both expressed per kg dry peat soil mass, and per microbial C mass (Fig. 5, Table 3). Estimated microbial N-immobilization was considerably higher in rich fens than in *Sphagnum*-fens per kg dry peat soil and per microbial C mass. The microbial N-immobilization rates in rich fens could even be up to 82–98% of the gross N-mineralization.

Treatment had a significant effect on net N-mineralization when expressed per kg dry peat soil, per microbial C mass, and per volume peat soil (Fig. 4, Table 3). According to a significant interaction effect of fen type*treatment, the two different fen types respond differently to treatment. Upon aeration, net N-mineralization in rich fens was on average 9.7 times higher than under anaerobic conditions when expressed per kg dry peat and on average 3.8 times higher when expressed per volume peat soil. In *Sphagnum*-fens, treatments did not significantly affect the net N-mineralization rate. Also estimated gross N-mineralization per kg dry peat soil

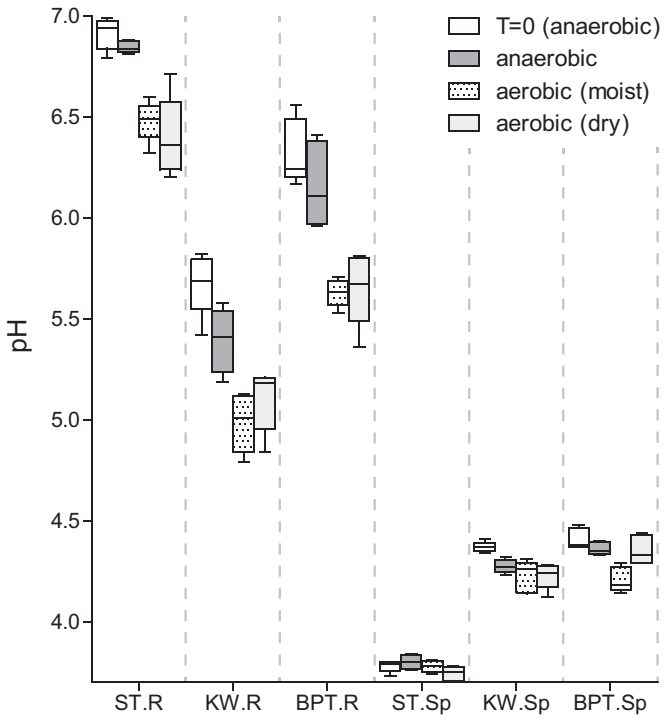

Fig. 2. Box plots showing soil pH-H_2O values of samples from the six different study sites for the different treatments (n = 5). ST.R = Stobbenribben rich fen, KW.R = Kiersche Wiede rich fen, BPT.R = Binnenpolder Tienhoven rich fen, ST.Sp = Stobbenribben *Sphagnum*-fen, KW.Sp = Kiersche Wiede *Sphagnum*-fen, BPT.Sp = Binnenpolder Tienhoven *Sphagnum*-fen. Upper and lower quartiles are indicated, as well as whiskers showing minimum and maximum values. Significant effects of fen type and treatment are indicated in Table 3.

was significantly affected by treatments, and given a significant interaction effect of fen type*treatment, the effect of aeration and desiccation on gross mineralization was again related to rich fen peat rather than to *Sphagnum*-peat. However, no significant interaction effect of fen type*treatment on microbial N-immobilization per kg dry peat soil was detected, which means that the effect of treatments on N-immobilization did not differ between rich fen peat and *Sphagnum*-peat.

The three rich fen locations responded differently with respect to their net N-mineralization rates upon treatments (Fig. 4). The microbial biomass showed a relatively high increase in the BPT rich fen, but not in the ST and KW rich fens, where the increase of net N-mineralization per kg peat soil upon aeration was due to increased microbial efficiency rather than increase of microbial biomass. In all three rich fens, gross N-mineralization increased upon aeration, but microbial immobilization increased only in the BPT rich fen. Upon desiccation, gross N-mineralization per microbial biomass C increased considerably especially at the BPT rich fen. However, due to a concomitant increase of the microbial N-immobilization per unit microbial C mass, the increase of net N-mineralization per kg dry soil and per volume peat soil was relatively limited.

3.2.4. Phosphorus cycling

The overall effect of treatment on net P-release was significant (Fig. 6, Table 3). The net P-release was negative under moist anaerobic and moist aerobic incubation, which means that in all of the fens there was net P-immobilization. However, after the soil samples dried out completely, net P-release increased considerably per kg dry peat soil, per microbial C mass and per volume peat soil. When expressed per kg dry peat soil, the effect of desiccation was similar for both rich fens and *Sphagnum*-fens, as indicated by a non-significant interaction effect of fen type*treatment. However, when expressed per microbial C mass the net P-release upon desiccation was higher in *Sphagnum*-peat. When expressed per volume peat soil, the net P-release was higher in the rich fens due to the higher bulk density, especially in the ST and KW rich fen. There seemed to be a shift in composition of the microbial population upon desiccation, because both the increase of DOC and PO_4 concentrations were relatively higher than the increase of inorganic N-concentrations upon desiccation in comparison to the other treatments.

4. Discussion

4.1. Does aeration lead to severe acidification?

One of the main questions with regard to water level drawdown is whether stimulation of aerobic oxidation processes leads to severe acidification and subsequently to vegetation changes. Lowering of pH as a result of water level drawdown is assumed to be temporary. When the water level is increased again, most of the protons produced will most likely be consumed due to the anaerobic reduction of alternative electron acceptors (Loeb et al., 2008). However, a drop in pH may temporarily lead to favorable conditions for establishment of *Sphagnum* spp., which is a threat to typical rich fen vegetation (Kooijman, 2012). In the ST rich fen, which is the most Ca-rich location, pH values did not drop below 6.0, which seems to be a critical value for rich fens dominated by *S. scorpioides* (Kooijman, 2012). However, in the KW and BPT rich fens, which have lower Ca-concentrations, pH values dropped to respectively 5.0 and 5.6, indicating that *Sphagnum* may get a competitive advantage.

4.2. Anaerobic respiration in rich fens versus Sphagnum-fens

Anaerobic respiration rates per kg dry peat soil did not differ between rich fens and *Sphagnum*-dominated fens, which is not consistent with previous work, in which decomposition rates per mass peat soil were generally lower in *Sphagnum*-dominated fens than in rich fens under moist anaerobic conditions (e.g. Farrish and Grigal, 1988). In these studies, the low decomposition rate of *Sphagnum*-peat has been attributed to several *Sphagnum*-specific characteristics, such as acidification (Verhoeven et al., 1990) and chemical composition (Belyea, 1996; Aerts et al., 1999). Cell walls of *Sphagnum*-litter contain phenolic compounds that would inhibit the activity of microorganisms involved in decomposition processes because of their recalcitrant nature and antibiotic properties (Van Breemen, 1995; Aerts et al., 2001). As the activity of phenol oxidase is limited under anaerobic conditions (Freeman et al., 2004), phenolics may accumulate and inhibit more general degradative enzymes such as glucosidases, phosphatases and sulphatases (Freeman et al., 2001), leading to reduced breakdown of organic matter (Fenner and Freeman, 2011). However, in view of the fact that anaerobic respiration rates per kg d.w. between fen types did not differ in this study, one may wonder whether these *Sphagnum*-specific characteristics really are determining the respiration rates under anaerobic conditions. When expressed per volume peat soil however, respiration rates were indeed higher in rich fens, but this was due to the higher bulk density in rich fens than in *Sphagnum*-fens.

The respiration rate per microbial biomass C in rich fens was lower than in *Sphagnum*-fens, which may be pH-related. Enwall et al. (2007) found a negative correlation between soil pH and the microbial metabolic quotient or also expressed as qCO_2 (respiration-to-biomass ratio), indicating a decreased efficiency of heterotrophic microorganisms to convert organic carbon into microbial biomass in rather acidic soils. This would explain the high

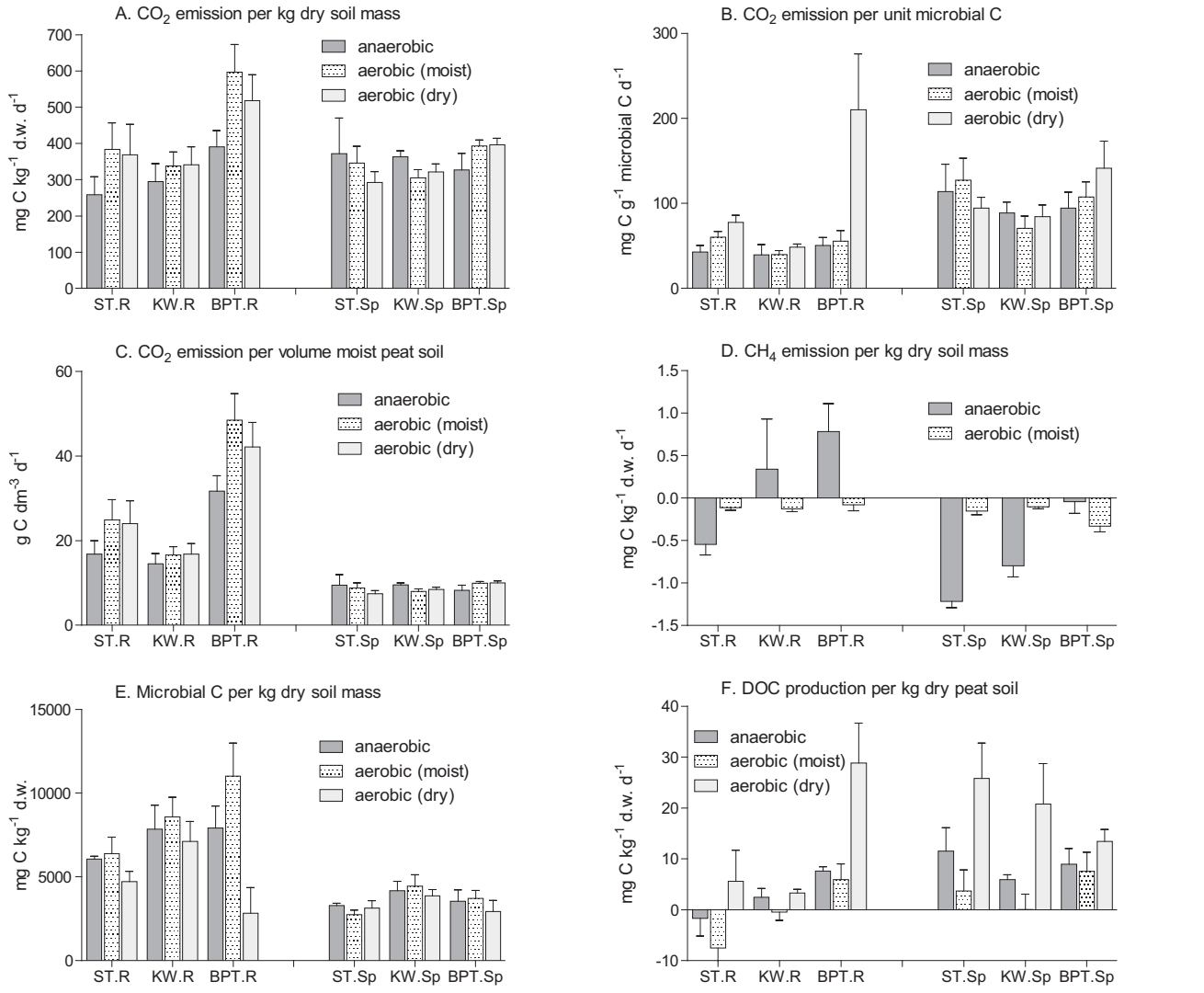

Fig. 3. Average fluxes of CO_2 (A, B, C), fluxes of CH_4 (D), microbial C (E) and DOC production (F) under anaerobic, moist aerobic and dry aerobic conditions for samples from the six different study sites (n = 5). Positive fluxes indicate release. ST.R = Stobbenribben rich fen, KW.R = Kiersche Wiede rich fen, BPT.R = Binnenpolder Tienhoven rich fen, ST.Sp = Stobbenribben *Sphagnum*-fen, KW.Sp = Kiersche Wiede *Sphagnum*-fen, BPT.Sp = Binnenpolder Tienhoven *Sphagnum*-fen. Standard deviations are indicated. Significant effects of fen type and treatment are indicated in Table 3.

respiration rate per microbial biomass C in *Sphagnum*-fens. Moreover, this lower respiration rate per microbial biomass C in rich fens seems to be compensated for by a larger number of microorganisms in rich fens than in *Sphagnum*-fens.

The negative CH_4 fluxes for all soils under initial anaerobic conditions indicate net uptake/consumption of CH_4 within the system, which has also been observed in previous research (Yavitt et al., 1990; Danevčič et al., 2010). Low or even negative emission rates may reflect methane oxidation by microbial communities associated with living and dead *Sphagnum* and other moss species (Raghoebarsing et al., 2005; Liebner et al., 2011), and may also reflect suppression of methanogenesis by other electron acceptors, because reduction of e.g. nitrogen is yielding a higher amount of Gibbs free energy (Stumm and Morgan, 1996). High soil N-concentrations have frequently been linked to decreases in methanogenesis (Bridgham and Richardson, 1992; Bender and Conrad, 1994). This may to some extent explain the persistent negative methane emission rates for both rich fen and *Sphagnum*-fen in the N-rich ST location. The high potential for microbial communities associated with *Sphagnum*-peat to oxidize CH_4 and reduce the emission of this greenhouse gas to the atmosphere (Raghoebarsing et al., 2005) is reflected in this study.

4.3. Different response of respiration to aeration and desiccation between fen types

Carbon respiration generally increases upon aeration of peat soils (e.g. Moore and Knowles, 1989; Freeman et al., 1993; Oechel et al., 1998; Blodau and Moore, 2003; Danevčič et al., 2010; Fenner and Freeman, 2011). In this study, aeration indeed led to increased respiration, but only in rich fens. The ratio of microbial soil respiration to microbial biomass (qCO_2) can be used as a measure of changes in microbial biomass in response to disturbance, in which the index supposedly declines during succession/ecosystem development, and increases during disturbance (Wardle and Ghani, 1995). Upon desiccation, the microbial soil respiration per microbial biomass C increased in the rich fens, indicating reduced microbial efficiency. In the *Sphagnum*-fens however this was not the case. Decomposition and respiration can be limited by oxygen deficiency, but also by litter quality and enzyme activity

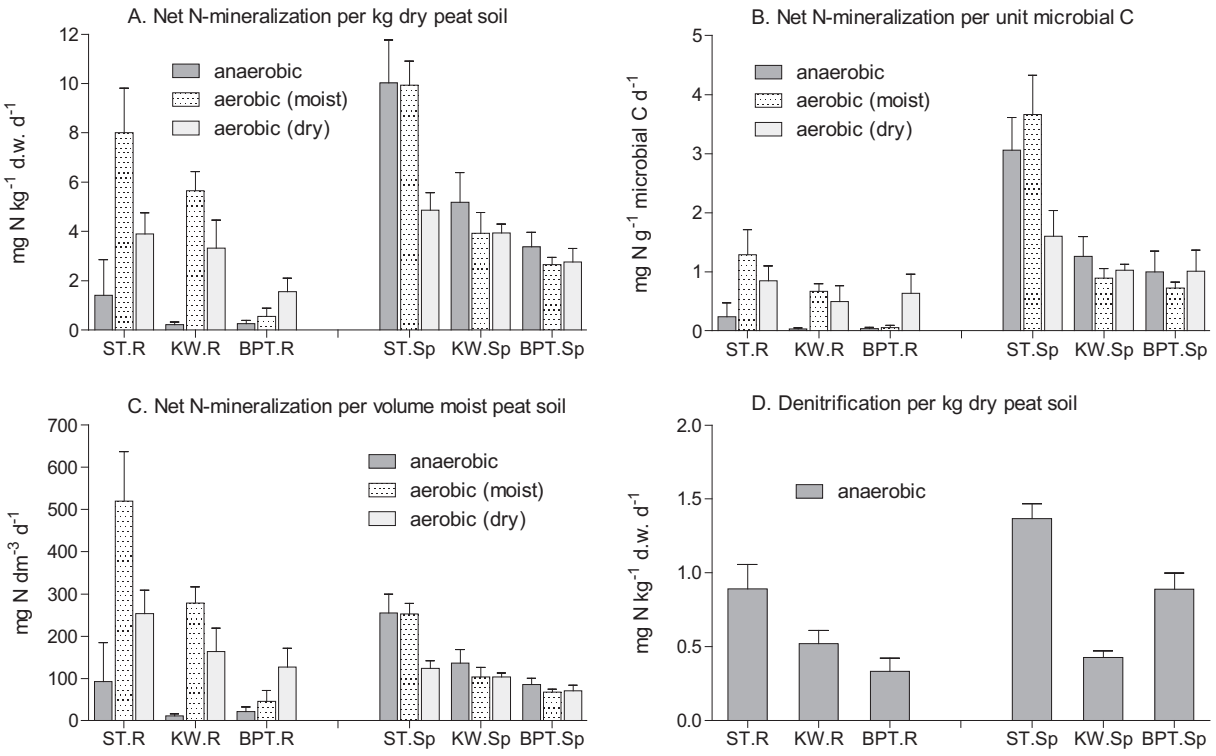

Fig. 4. Rates of net N-mineralization (A, B, C) under anaerobic, moist aerobic and dry aerobic conditions, and rates of anaerobic denitrification (D) for samples from the six different study sites (n = 5). ST.R = Stobbenribben rich fen, KW.R = Kiersche Wiede rich fen, BPT.R = Binnenpolder Tienhoven rich fen, ST.Sp = Stobbenribben *Sphagnum*-fen, KW.Sp = Kiersche Wiede *Sphagnum*-fen, BPT.Sp = Binnenpolder Tienhoven *Sphagnum*-fen. Standard deviations are indicated. Significant effects of fen type and treatment are indicated in Table 3.

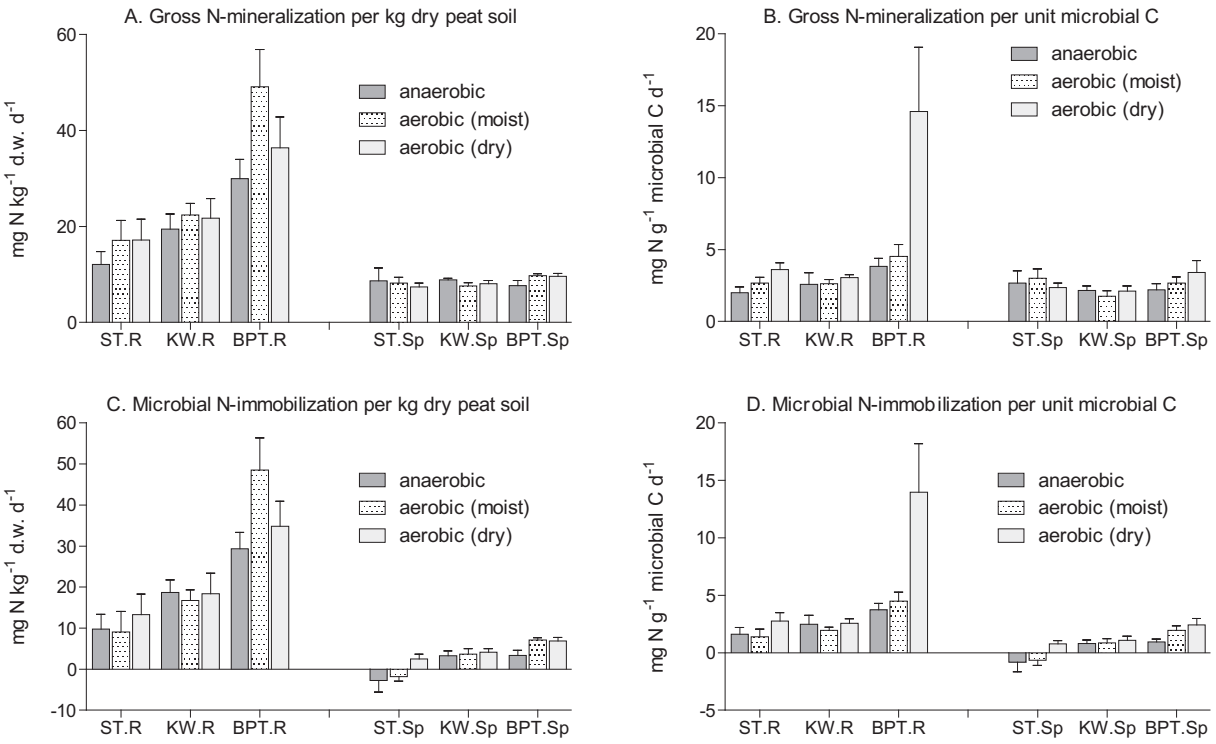

Fig. 5. Rates of gross N-mineralization (A, B) and N-immobilization (C, D) for samples from the six different study sites under different incubation conditions (n = 5). ST.R = Stobbenribben rich fen, KW.R = Kiersche Wiede rich fen, BPT.R = Binnenpolder Tienhoven rich fen, ST.Sp = Stobbenribben *Sphagnum*-fen, KW.Sp = Kiersche Wiede *Sphagnum*-fen, BPT.Sp = Binnenpolder Tienhoven *Sphagnum*-fen. Standard deviations are indicated. Significant effects of fen type and treatment are indicated in Table 3.

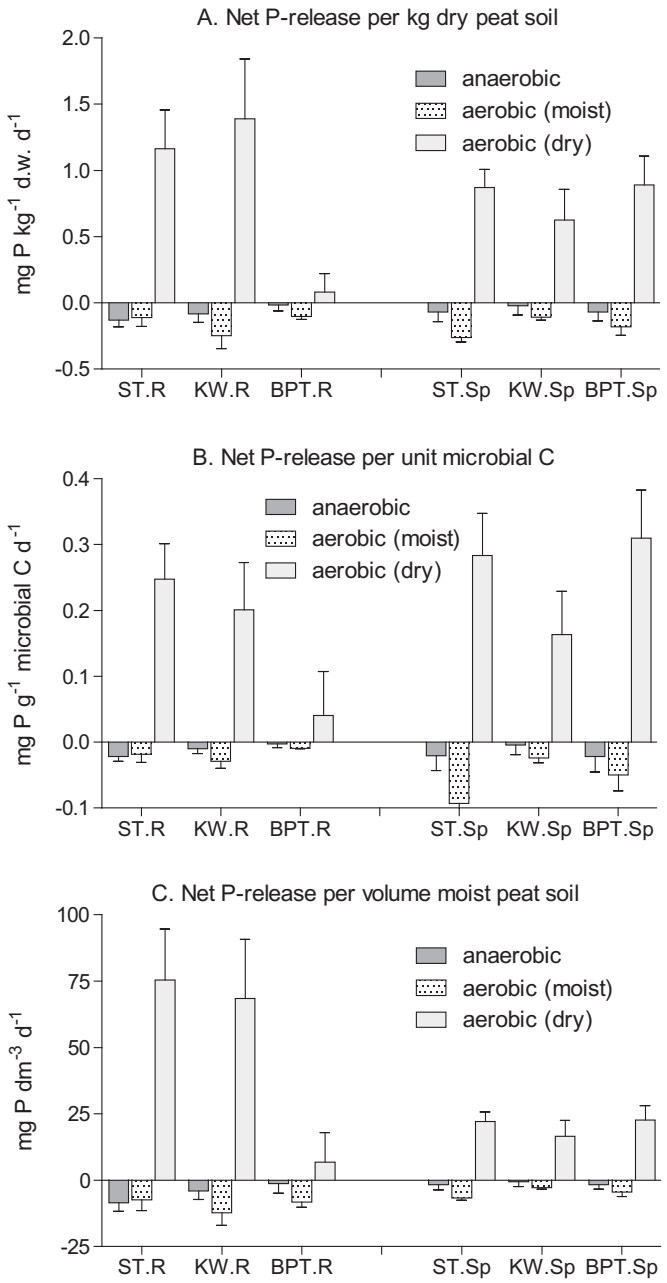

Fig. 6. Rates of net P-release for samples from the six different study sites under different incubation conditions (n = 5). ST.R = Stobbenribben rich fen, KW.R = Kiersche Wiede rich fen, BPT.R = Binnenpolder Tienhoven rich fen, ST.Sp = Stobbenribben *Sphagnum*-fen, KW.Sp = Kiersche Wiede *Sphagnum*-fen, BPT.Sp = Binnenpolder Tienhoven *Sphagnum*-fen. Standard deviations are indicated. Significant effects of fen type and treatment are indicated in Table 3.

(Freeman et al., 2001). In *Sphagnum*-fens, decomposition is probably not only limited by oxygen deficiency, but also by the high concentrations of phenolic compounds in *Sphagnum*-litter (Van Breemen, 1995; Aerts et al., 2001). In spite of the fact that in all fens aeration presumably stimulated the activity of phenol oxidase, the enzyme responsible for the breakdown of phenolic compounds (Fenner and Freeman, 2011), aeration did not lead to increased respiration rates in *Sphagnum*-fens, probably because *Sphagnum*-litter contained too many phenolic compounds. Rich fens presumably contain lower concentrations of phenolic compounds. In rich fens, stimulation of phenol oxidase by aeration may therefore have led to phenol-concentrations that are low enough for other degradative enzymes in rich fens to be active, such as glucosidase and phosphatase (Freeman et al., 2004), resulting in increased respiration upon aeration in rich fens. These mechanisms should be further investigated.

4.4. The response of DOC production upon aeration and desiccation

Rates of DOC production did not follow the clear pattern as observed for CO_2 production, probably because DOC can be both sink and source of carbon and therefore can be affected by many factors. The slight decrease of DOC concentrations as a result of aeration seems in accordance with Glatzel et al. (2003), who showed that DOC concentrations are often higher under anaerobic conditions than under aerobic conditions, because of accumulation of intermediate metabolic products instead of formation of CO_2. However, DOC production may also decrease upon aeration due to increased biological activity and increased consumption of DOC as a substrate for respiration (Pastor et al., 2003).

Upon total desiccation however, DOC production increased considerably. This may suggest an increase in overall decomposition, as documented in previous work (Mitchell and McDonald, 1992; Olde Venterink et al., 2002), but in our study respiration did not increase. The increased DOC production may instead be related to mortality of microbes, as a result of water shortage, by which cellular constituents are released. This idea was supported by a decreasing microbial C mass upon total desiccation.

4.5. Anaerobic N-mineralization and N-immobilization in rich fens versus Sphagnum-fens

For the connection to plant production in relation to nutrient availability for roots, nutrient mineralization rates per unit volume are most important. This study clearly showed higher net N-mineralization rates per unit volume under anaerobic conditions in *Sphagnum*-fens than in rich fens. Also, when expressed per kg dry peat, anaerobic net N-mineralization rates were significantly higher in *Sphagnum*-peat, which is in conformity with results from previous studies (Verhoeven and Arts, 1987; Verhoeven et al., 1988, 1990; Updegraff et al., 1995), but does not correspond with the general idea that conditions for litter decay and mineralization are more favorable in mineral-rich than in mineral-poor wetlands (Bayley et al., 2005). Also, net N-mineralization rates per microbial C mass were higher in *Sphagnum*-dominated fens than in rich fens, which corresponds well with previous experiments carried out by Kooijman and Hedenäs (2009).

These differences in anaerobic net N-mineralization rates between both fen types cannot be related to denitrification, because anaerobic denitrification rates in all fens were relatively low compared to the high net N-mineralization rates as measured in *Sphagnum*-peat. Other N-removing pathways, such as dissimilatory nitrate reduction to ammonium (DNRA) or anaerobic ammonium oxidation (anammox) (Burgin and Hamilton, 2007), are not likely to be seriously affecting the measured net N-mineralization either, since the quantitative contribution of these pathways in semi-terrestrial fens are assumed to be relatively small compared to denitrification (White and Reddy, 2009).

The higher anaerobic net N-mineralization per kg dry peat, per microbial C mass en per volume peat soil in *Sphagnum*-fens cannot be explained by differences in gross N-mineralization either, as estimated gross N-mineralization was higher in rich fens than in *Sphagnum*-fens. Since the net N-mineralization rate is a net result of gross N-mineralization and microbial N-immobilization, microbial immobilization characteristics are often determinative for the N-availability for plants (Robertson and Groffman, 2007). In this

study, estimated microbial N-immobilization rates were significantly higher in rich fens than in *Sphagnum*-fens, which probably explains the differences in net N-mineralization between fen types. Microbial decomposition of organic matter is regulated by a variety of heterotrophic bacteria and fungi (Coulson and Butterfield, 1978), and changes in microbial N-demand may be associated with shifts in bacterial and fungal composition occurring over pH gradients (Kooijman et al., 2008; Kooijman and Hedenäs, 2009). In rich fens, bacteria are generally more abundant and active in anaerobic decomposition, while in acidic peatlands the bacterial population and its activity are generally limited, and fungal activity becomes more dominant (Winsborough and Basiliko, 2010). Bacteria generally have a lower C:N biomass ratio and a higher N-demand than fungi (Hassink et al., 1993; Robertson and Groffman, 2007), which is possibly caused by the fact that bacteria use amino acids rather than carbohydrates for osmoregulation (Kuehn et al., 1998). Considering these ideas, it is rather likely that the higher N-immobilization rates per microbial C mass as estimated in our study may provide an explanation for the lower net N-mineralization rates in rich fen peat compared to *Sphagnum*-peat under anaerobic conditions.

4.6. Different response of net N-mineralization to aeration and desiccation between fen types

Aeration in wetlands due to drought is generally assumed to result in an increase of net N-mineralization rates per kg peat (Grootjans et al., 1985, 1986; Williams and Wheatley, 1988; Bridgham et al., 1998; Updegraff et al., 1995; Olde Venterink et al., 2002; Holden et al., 2004). In this study, aeration and desiccation only resulted in increased net N-mineralization per kg peat and per volume peat for the rich fens, not only because of increased microbial biomass, but also because of increased net N-mineralization per unit microbial C. Interestingly, net N-mineralization rates in *Sphagnum*-fens were not affected by increased availability of oxygen. This striking difference in response between both fen types is probably caused by differences in concentrations of phenolic compounds and degradative enzymes, just as in the case of the respiration results. It may be that only in rich fens the concentrations of phenolic compounds are low enough to allow other enzymes to be active, resulting in increased net N-mineralization upon aeration and desiccation. These mechanisms should be further investigated.

4.7. The effect of aeration and desiccation on net P-release

The impact of aeration and desiccation on processes concerning net P-release is rather complicated, because apart from mineralization processes, there are redox-sensitive processes of chemical P-binding. For P it has been shown by Olde Venterink et al. (2002) that aeration and increased decomposition rates do not necessarily lead to an increased net P-release. We confirm these findings, as we did not find any significant differences in net P-release upon aeration, even though respiration rates increased in rich fens. This may be caused by the fact that released PO_4 can be bound immediately after mineralization, for example as Fe-phosphates (Patrick and Khalid, 1974; Richardson, 1985) or Ca-phosphates (Boyer and Wheeler, 1989; Reddy et al., 1993). Since the mobilization and immobilization of Fe-phosphates is redox-sensitive (Patrick and Khalid, 1974; Lijklema, 1980; Boström et al., 1982; Richardson, 1985), oxidation processes under aerobic conditions presumably led to the formation of Fe(III) oxides and hydroxides, which may have reduced net P-mobilization.

In contrast to aeration, full desiccation led to an enormous increase of the net P-release. These results are in contrast with a potential decrease due to redox sensitive Fe–P complexation. Microbial mortality resulting from drought, as supported by the reduced microbial biomass C upon desiccation, may have resulted in a net increase of extractable PO_4 concentrations. It seems though that also a change in microbial population took place upon desiccation, because both the increase of DOC and PO_4 concentrations were relatively higher than the increase of inorganic N-concentrations upon desiccation in comparison to the other treatments. Additional research is required, focusing on the balance between biogeochemical P-binding and microbial P-mobilization as a result of drought.

4.8. Implications for the field situation

Water level drawdown initially leads to an increase in oxygen availability. Due to aerobic oxidation processes, pH values decreased after aeration and further desiccation. Although the pH will probably increase again during subsequent rising of the water level (Loeb et al., 2008), a temporary decrease in pH may lead to suitable conditions for dominance by *Sphagnum*-species that further acidify the habitat, which on its turn can lead to severe decline of the rich fen bryophyte vegetation. Moreover, aeration was shown to lead to increased N-availability per volume peat soil in the root zone of rich fens, which will possibly promote the degradation of rich fens because of increased encroachment of graminoid species at the expense of characteristic brown moss and slow-growing vascular species.

Severe desiccation should be avoided in any case from a management perspective, because this not only leads to increased net N-mineralization, but also to considerable net P-release and net DOC production per volume peat soil in the root zone. High concentrations of P are obviously a threat to nutrient-poor and predominantly P-limited rich fen habitats, and increased net DOC production can have negative chemical and ecological consequences, as it alters acid-base chemistry and P and N availability, and leads to lower carbon sequestration rates (Turetsky, 2003). Therefore, periods of low water levels are definitely undesirable with regard to the conservation of rich fens.

With regard to the conservation of *Sphagnum*-dominated fens, aeration as a result of water level drawdown did not seem to lead to increased respiration and net N-mineralization per volume peat soil in the root zone. Further desiccation, however, should also be avoided in *Sphagnum*-dominated fens, because of increased P-release and net production of DOC per volume peat soil.

However, it is important to emphasize that the laboratory conditions in this study are not completely identical to the field situation, since capillary action in peat often leads to relatively wet soils even if drought leads to lowering of the water table (Clymo and Hayward, 1982). The elasticity of a peat soil furthermore causes the surface to follow the water level when it moves down, a phenomenon called ‘moor-atmung’ or ‘mire-breathing’ (Ingram, 1983), which can also keep the surface of a peatland moist. The incubation results are nevertheless useful to assess the effects of drought in the field, since the oxygen availability can certainly increase significantly in periods of more than two months of relative drought. Redox profiles, that have been measured over time in peat soils from both a rich fen and a *Sphagnum*-fen in Stobbenribben, indicate that such periods of drought are common in the upper 10 cm of the soil (see Appendix A, Supplementary data).

4.9. Suggestions for further research

This experiment not only showed how net N- and P-mineralization rates are influenced by microbial immobilization, but also

showed that these processes highly depend on the ANC of the peat. In order to get a more detailed understanding of microbial immobilization, stable isotope studies are suggested, which should focus on microbial growth and the C and N pathways in the microbial biomass of both rich fen soils and *Sphagnum*-dominated soils. In addition, more frequent measurements during incubation would provide more detailed information about the exact course of respiration, mineralization and immobilization rates over time. Due to the extensive experimental design, this was not possible in our study. Furthermore, additional measurements of litter quality and litter composition of *Sphagnum* and typical rich fen mosses, such as *S. scorpioides* and *H. vernicosus*, would reveal to what extent differences in chemical litter composition determine decomposition rates.

5. Conclusions

Our results show that under anaerobic conditions, net N-mineralization rates are lower in rich fens than in *Sphagnum*-fens, which seems to be due to significantly higher rates of microbial N-immobilization in rich fens. Although this phenomenon has been described in previous studies, it has never been demonstrated by estimating microbial N-immobilization. We suggest that these differences in net N-mineralization reflect differences in microbial N-demand and N-immobilization between the two fen types, associated with differences in bacterial and fungal dominance. The effects of aeration clearly differ between rich fens and *Sphagnum*-fens with respect to respiration and net N-mineralization. In rich fens, aeration seems to lead to increased respiration and net N-mineralization, while this was not the case in *Sphagnum*-peat. We therefore postulate that the biogeochemical effects of aeration as a result of moderate drought may be less severe in *Sphagnum*-fens, because the concentrations of phenolic compounds in *Sphagnum*-dominated peat are so high that activation of phenol oxidase by aeration only has a relatively limited effect. Furthermore, we showed that net P-release and DOC production increased significantly upon severe desiccation, which may be due to induced microbial die-off and/or a change in microbial composition. With respect to fen conservation management, the results of our study show that in particular in rich fens even moderate drought, during which oxygen availability increases but the peat is still moist, should be avoided because of acidification and increased N-availability, leading to dominance of graminoid species at the expense of characteristic brown moss and slow-growing vascular species. Above all, however, severe drought has a negative impact in both rich fens and *Sphagnum*-fens, not only because of direct adverse effects on wetland vegetation, but also because of severe increase of P-availability, leading to rapid succession, and possible loss of peat due to DOC-production.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2013.10.023.

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