Biogeosciences

Effects of N and P fertilization on the greenhouse gas exchange in two northern peatlands with contrasting N deposition rates

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Abstract. Peatlands are important ecosystems in the context of biospheric feedback to climate change, due to the large storage of organic C in peatland soils. Nitrogen deposition and increased nutrient availability in soils following climate warming may cause changes in these ecosystems affecting greenhouse gas exchange. We have conducted an N and P fertilization experiment in two Swedish bogs subjected to high and low background N deposition, and measured the exchange of CO_2, CH_4 and N_2O using the closed chamber technique. During the second year of fertilization, both gross primary production and ecosystem respiration were significantly increased by N addition in the northernmost site where background N deposition is low, while gross primary production was stimulated by P addition in the southern high N deposition site. In addition, a short-term response in respiration was seen following fertilization in both sites, probably associated with rapid growth of nutrient-limited soil microorganisms. No treatment effect was seen on the CH_4 exchange, while N_2O emission peaks were detected in N fertilized plots indicating the importance of taking N_2O into consideration under increased N availability. In a longer term, increased nutrient availability will cause changes in plant composition, which will further act to regulate the peatland greenhouse gas exchange.

1 Introduction

Peatlands have over the last millennia accumulated vast amounts of carbon (C) in their soils, amounting to ca. one-third of the world total soil C pool (Gorham, 1991; Turunen et al., 2002). The average C accumulation rates in peatlands have been estimated to be 15–30 g C m^{-2} yr^{-1}

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(Gorham, 1991; Tolonen and Turunen, 1996; Turunen et al., 2002). Peatland vegetation takes up atmospheric carbon dioxide (CO_2) through gross primary production (GPP). Carbon dioxide is subsequently released back to the atmosphere via autotrophic and heterotrophic respiration, collectively referred to as ecosystem respiration (R_{eco}). The net ecosystem exchange (NEE) constitutes the sum of these two opposing fluxes. Apart from the CO_2 exchange, peatlands are also a significant source of methane (CH_4). Methane is produced in the waterlogged, anaerobic subsurface zone by methanogenic archaea, while part of it is consumed in the aerobic surface zone by methanotrophic bacteria (Whalen, 2005). The C sink functioning of peatlands is primarily explained by limited decomposition rates due to the prevailing cool, anaerobic and nutrient-poor conditions (Clymo, 1984). Due to their low pH and nutrient status, peatlands generally show a non-significant nitrous oxide (N_2O) exchange (Martikainen et al., 1993).

During the last decades, increased nitrogen (N) deposition in many parts of the world has increased the N input to the ecosystems. In addition, global warming will lead to increased mineralization rates, which will release more nutrients for plant uptake (Rustad et al., 2001; Mack et al., 2004). Nutrient-poor peatlands (bogs) are generally dominated by *Sphagnum* mosses. They have the ability to intercept airborne nutrients, providing a competitive advantage over vascular plants that rely on nutrient uptake by roots (Malmer and Wallén, 2005). However, at high levels of N input the *Sphagnum* filter will become saturated, and additional N will leach down to the vascular plant root zone enhancing growth of vascular plants (Lamers et al., 2000; Rydin and Jeglum, 2006). An increased abundance of vascular plants may reduce C sequestration due to the shift towards more easily decomposable litter (Berendse et al., 2001; Malmer and Wallén, 2005). Previous studies have also shown that very high rates of N deposition may lead to accumulation of toxic NH$_4^+$ in the *Sphagnum* cell resulting in growth reduction; Limpens

and Berendse (2003) found that *Sphagnum* growth was reduced at deposition rates of $80\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$, but not at $40\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$.

Fungi and bacteria are the most important decomposers in peatlands (Coulson and Butterfield, 1978; Bragazza et al., 2006). Initial rates of microbial decomposition are generally correlated with substrate N and P concentrations; it can thus be expected that microbial breakdown increases in the short-term if the nutrient limitation is reduced, leading to increased rates of CO_2 and CH_4 effluxes (Aerts and de Caluwe, 1999). In an experiment carried out in a drained fen in France, N addition led to a steady increase in total microbial biomass (Gilbert et al., 1998). Bragazza et al. (2006) investigated bogs in a natural gradient of N deposition from 2 to $20\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$, and found enhanced decomposition rates under higher N deposition. This was explained by the removal of N constraints on microbial metabolism and increased litter peat quality. The microbial community in peatlands is likely to respond more rapidly than plants to changes such as nutrient addition, because of their higher turnover rates.

Methane emissions from peatlands can be affected in several ways if subjected to increased nutrient availability. Some soils show inhibitory effects of N addition on CH_4 oxidation rates (Crill et al., 1994; Christensen et al., 1999; Kravchenko, 2002), while others show minor or no effect (Gulledge et al., 1997; Saarnio and Silvola, 1999). The addition of nitrate may also inhibit methanogenesis e.g. by competition for hydrogen or due to toxicity of denitrification products to the methanogens (Conrad, 1999). In a longer time perspective, CH_4 emissions from peatlands can be increased if the abundance of vascular plants increases, through their effects on the net CH_4 flux by providing gas conduits (Joabsson et al., 1999) and by releasing fresh, organic compounds to the rhizosphere serving as substrate for CH_4 formation (Ström et al., 2003). However, one of the roles played by root exudates is to facilitate nutrient uptake (Walker et al., 2003), which could mean diminishing root exudation with increasing nutrient availability. The net effect of nutrients on the CH_4 exchange is likely dependent on peatland type and site-specific properties (Keller et al., 2006). Increasing the amount of N in an ecosystem also increases the potential for N_2O emission, both through nitrification and denitrification, in accordance with the "hole-in-the-pipe" conceptual model by Firestone and Davidson (1989).

Previous studies have reported diverse fertilization effects on the peatland gas exchange. Bubier et al. (2007) found decreased GPP with the highest levels of fertilization, but no effects on R_{eco} in an ombrotrophic bog. Saarnio et al. (2003) found minor increases in GPP in N fertilized plots in a boreal fen, but no effect on annual C balance. In contrast, Mack et al. (2004) reported increases in net primary production but major decreases in soil C storage in Alaskan tundra after 20 years of fertilization. Keller et al. (2005) found no major effects on soil C cycling after six years of N and P fer-

tilization in a temperate fen. Regarding CH_4, Granberg et al. (2001) found that N addition slightly decreased emissions, while Nykänen et al. (2002) found increased emissions associated with increased sedge cover.

In this study, we investigate the effects of fertilization on the exchange of three greenhouse gases (CO_2, CH_4, N_2O), in two ombrotrophic peatlands. To achieve this, we have added N and P to two contrasting bog ecosystems; a south-Swedish temperate bog with high rates of atmospheric N deposition (Fäjemyr) and a north-Swedish subarctic bog (Storflaket) with low atmospheric N deposition, and performed greenhouse gas measurements in situ using the closed chamber technique. To our knowledge, this is the first study that takes all three major greenhouse gases into account in a peatland fertilization experiment. We hypothesize that we will observe: (1) increased CO_2 component fluxes (GPP, R_{eco}) in response to N addition in Storflaket and P addition in Fäjemyr; (2) limited effects on CH_4 exchange; and (3) increased N_2O emissions as a result of increased N availability.

2 Materials and methods

2.1 Site description

The south Swedish site, Fäjemyr, is a temperate, ombrotrophic bog (lat: $56°15'\,$N, long: $13°33'\,$E, alt: $140\,\mathrm{m}$). Long-term mean annual temperature and precipitation (1961–1990) are $6.2°\,$C (min January: $-2.4°\,$C, max July: $15.1°\,$C) and $700\,\mathrm{mm}$, respectively. The wet and dry N deposition in the area is estimated to ca. $15\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ (Fig. 1). The water table is generally below the surface, which causes the topographical pattern of Fäjemyr to be dominated by hummocks, lawns and carpets. Hollows and open pools are scarce. These fairly dry conditions allow the existence of dwarf shrubs in the study area, mainly *Calluna vulgaris* and *Erica tetralix*. Moss layer is dominated by *Sphagnum magellanicum* and *S. rubellum*. Sedges, mainly *Eriophorum vaginatum*, are also prevalent.

Storflaket is a subarctic bog located in northernmost Sweden ($68°20'\,$N, $18°58'\,$E, alt: $380\,\mathrm{m}$) close to the Abisko Scientific Research Station. Long-term mean annual temperature and precipitation are $-0.8°\,$C and $304\,\mathrm{mm}$, respectively. The mire is underlain by permafrost with an active layer of 60–70 cm in the study area in late summer (Åkerman and Johansson, 2008). In this area, N deposition is ca. $2\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ (Fig. 1). The experimental area can be categorized as a dry to semi-dry ombrotrophic habitat. The vegetation is dominated by *Sphagnum* mosses (*S. fuscum* and *S. balticum*), dwarf shrubs (*Empetrum nigrum*, *Andromeda polifolia*), *Rubus chamaemorus* and *E. vaginatum*.

2.2 Fertilization

Fertilization began in both sites in 2006. In Fäjemyr, 16 plots ($1\times2\,\mathrm{m}$) were randomly assigned one of the following four
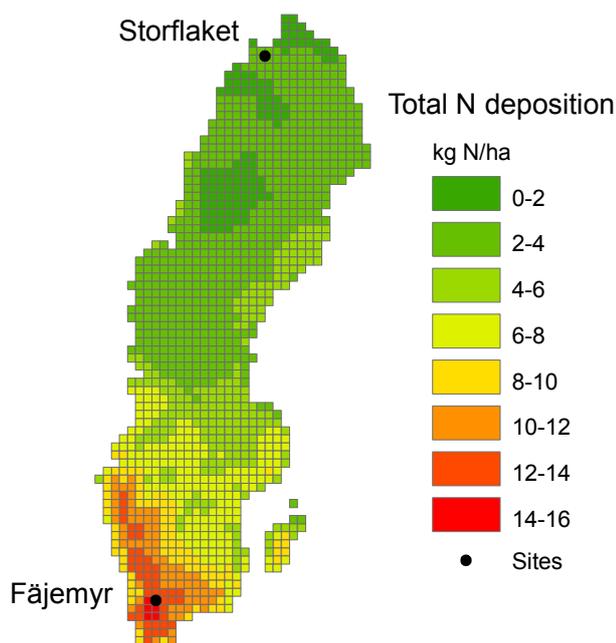
Fig. 1. Total N deposition (dry and wet $NO_x + NH_x$ deposition) in Sweden during 2005. Data from SMHI (Swedish Meteorological and Hydrological Institute) MATCH model (Persson et al., 2004).

treatments (four replicates): high nitrogen (HN) addition, phosphorus (P) addition, nitrogen and phosphorus (HNP) addition, and control (CL). There was one additional treatment in Storflaket: low nitrogen (LN) addition (20 plots in total). Fertilization took place three times per year; in spring, summer and autumn. The amount of nutrients given to the plots starting in spring 2006 equalled $40 \, kg \, N \, ha^{-1} \, yr^{-1}$ ($20 \, kg \, N \, ha^{-1} \, yr^{-1}$ in LN) and $0.5 \, kg \, P \, ha^{-1} \, yr^{-1}$. In 2007, the amount of P was increased to $4 \, kg \, P \, ha^{-1} \, yr^{-1}$, since soil water analyses showed that using this amount in the HNP treatment would more closely resemble the N:P ratio of mire water. Nutrients were given as NH_4NO_3 and $NaH_2PO_4 \times H_2O$ dissolved in mire water, and spread evenly over the plots using a watering can. The CL plots received unfertilized mire water. The total amount of water used in the fertilization equalled $6 \, mm \, yr^{-1}$. The amount of N added to the plots in the HN treatment is approximately three times higher than the deposition in Fäjemyr (and 20 times in Storflaket), however it can be compared with deposition rates of up to $50 \, kg \, N \, ha^{-1} \, yr^{-1}$ in central Europe (Aerts, 1997).

2.3 Flux measurements

Greenhouse gas (GHG) flux measurements were performed weekly to biweekly in Fäjemyr between March and November during 2007. In Storflaket, measurements were campaign based and concentrated around the fertilization events in 2007; one week in May, two weeks in June–July and one week in September. Greenhouse gas flux measurements in

connection with the fertilization events were performed on day 0, 1 (fertilization day), 2, 4, 7 and 14, in order to explore particularly short-term effects. In summer 2006, aluminium collars (depth: 20 cm) were inserted in each plot. The collars had grooves that were filled with water before GHG flux measurements to avoid gas leakage. Transparent chambers ($40 \times 40 \, cm$, height: 37 cm) equipped with a fan and a pressure vent were fitted on top of the collars during GHG flux measurements.

The flux measurements were carried out using a closed, flow-through chamber system. The system was equipped with a pump that continuously drew air from the chamber headspace through high density polyethylene tubing to the gas analysers at a rate of ca. $1 \, L \, min^{-1}$. Concentrations of CO_2 were measured using an infrared gas analyser (LI-820, LiCor Inc, USA). Methane and N_2O concentrations in Fäjemyr were measured using a photoacoustic multigas infrared gas analyser (Innova 1312, Innova AirTech Instruments A/S, Denmark). We used soda lime to remove CO_2 and a Nafion tubing (Perma Pure LLC, USA) to minimize H_2O fluctuations before sample air entered the Innova. To check the reliability and comparability of the CH_4 flux measurements, we sampled chamber headspace air in syringes (grab samples; three samples were taken during each measurement period) at the same time as the Innova analyses at two occasions (1 June and 12 September), and analysed them using a gas chromatograph (GC) at Lund University (Shimadzu GC 17A). We found that the agreement for reliable fluxes (see Sect. 2.5) was high ($r^2 = 0.89$, $n = 11$) with a close to 1:1 relationship between GC and Innova (regression equation: GC=0.94Innova+0.088). In Storflaket, CH_4 concentrations were measured using grab samples, which were subsequently analysed on a GC at Abisko Scientific Research Station (Shimadzu GC 14B) within one day. For each plot, three separate gas flux measurements were performed on each measurement occasion: (1) transparent chamber measurements of NEE during two minutes; (2) darkened chamber (covered by beaver nylon to inhibit photosynthesis) measurements of R_{eco} during two minutes; and (3) darkened chambers measurements of CH_4 (and N_2O in Fäjemyr) during ca. 25 min.

2.4 Ancillary measurements

In connection with the GHG flux measurements, soil temperature at 5 cm depth (T_s) using Tiny-loggers (T-0063, Amestec Oy, Finland) and water table depth (WTD) using perforated plastic tubes were measured from just outside the collars. Vegetation inventories (point-intercept method) were performed in July 2006 and July 2007 using a 50-point frame installed over each collar. Plant species abundance was sorted into the plant functional types (PFT) *Sphagnum* mosses, sedges and shrubs. Approximately 180 m from the fertilization experiment area in Fäjemyr, additional parameters such as air temperature, photosynthetic photon flux density

(PPFD) and WTD were continuously recorded in connection with an eddy covariance system (Lund et al., 2007).

2.5 Data handling and statistical analyses

The GHG flux rates were calculated from the change in gas concentration as a function of time during chamber closure. Gross primary production was calculated as the difference between time adjacent measurements with transparent and darkened chamber, respectively. For CH_4 and N_2O fluxes, the coefficient of determination (r^2) values for a linear regression of concentration against time had to be higher than 0.7 for the fluxes to be considered reliable. We have adopted the micrometeorological sign convention where negative flux values indicate gas uptake by the ecosystem, while positive values represent emission to the atmosphere.

All data was tested for normality using the one-sample Kolmogorov-Smirnov test before running any parametrical statistical tests. The evaluation of the fertilization effect on the GHG flux exchange was performed in the following ways:

– Repeated measures analysis of variance (RM-ANOVA) was used to test for treatment effects on GPP, R_{eco}, NEE and CH_4 exchange. Greenhouse gas flux measurements from all plots were temporally averaged for spring (March–May), summer (June–August) and autumn (September–November). Soil temperature, WTD and coverage of vascular plants, shrubs, sedges and *Sphagnum* mosses in each chamber were treated as covariates if significant ($p < 0.05$). RM-ANOVA was performed in SPSS 12.0.1 (SPSS Inc., 2003) using type III sums of squares (Bubier et al., 2007).

– To take diurnal and seasonal dynamics in the CO_2 exchange into account, the annual time series of GPP and R_{eco} in Fäjemyr were reconstructed for each plot separately using the following simple nonlinear models (Saarnio et al., 2003);

$$GPP = \frac{b_0 \times PPFD \times T_s}{b_1 + PPFD} \qquad (1)$$

$$R_{eco} = \exp(b_0 + b_1 \times T_s + b_2 \times WTD) \qquad (2)$$

where b_0, b_1 and b_2 are regression parameters. Stepwise regression was used to test whether T_s and WTD were significant variables in explaining respiration fluxes. Half-hourly readings of PPFD, T_s and WTD were derived from continuous measurements on the bog close to the measurement site (Lund et al., 2007). Measurements on day 0, 1 and 2 were averaged when computing the R_{eco} function to minimize temporal autocorrelation. The time series of GPP and R_{eco} were reconstructed between March and November for each plot. Subsequently, NEE was calculated as the sum of GPP and

R_{eco}. Treatment effects on the integrated CO_2 flux components and NEE was tested for using one-way analysis of variance (ANOVA), and difference from control was tested with two-sided Dunnett post hoc test.

3 Results

3.1 Vegetation

In the 2007 vegetation inventory, there were no significant differences with regards to plant functional types (i.e. *Sphagnum* mosses, sedges, shrubs) between the treatments, neither in Fäjemyr (ANOVA: sedges $p = 0.49$, shrubs $p = 0.68$, *Sphagnum* $p = 0.53$), nor in Storflaket (ANOVA: sedges $p = 0.62$, shrubs $p = 0.39$, *Sphagnum* $p = 0.93$). There was no significant change between 2006 and 2007 in any possible combination of PFT and treatment in Fäjemyr (t-test: $p > 0.05$), while in Storflaket, there was a significant increase of shrubs in HNP plots (t-test: $p = 0.04$).

Vegetation indices (number of hits in vegetation inventories of *Sphagnum*, vascular plants (includes all vascular plants), sedges, shrubs) were compared with annual averages of R_{eco}, NEE, GPP and CH_4 in each plot. Significant correlations in Fäjemyr were found between R_{eco} and shrubs ($r = 0.682$, $p = 0.004$), R_{eco} and vascular plants ($r = 0.622$, $p = 0.010$), GPP and shrubs ($r = -0.667$, $p = 0.005$), GPP and vascular plants ($r = -0.650$, $p = 0.006$) and CH_4 and sedges ($r = 0.755$, $p = 0.001$). In Storflaket, vascular plants correlated with R_{eco} ($r = 0.670$, $p = 0.001$), as well as GPP ($r = -0.648$, $p = 0.002$).

3.2 Short-term fertilization effect

An immediate short-term effect was generally seen in the R_{eco} measurements during the first days after nutrients were added. In Storflaket, N addition caused an instantaneous increase in R_{eco} (Fig. 2). Respiration was significantly higher than CL (two-sided Dunnett test: $p < 0.05$) on day 1 (fertilization day) in HNP plots in spring, in LN and HN plots in summer, and in LN and HNP plots in autumn. Respiration was also significantly higher in HN plots than in CL plots on day 2 in autumn. In Fäjemyr, R_{eco} was significantly higher in HN, HNP and P plots on day 1 in autumn. No such effect was seen for GPP or CH_4 emissions in neither of the two sites.

3.3 Exchange of N_2O

The N_2O exchange in Fäjemyr was generally close to zero, with both negative and positive fluxes. Interestingly, N_2O emission peaks of ca. $150\,\mu g\,N_2O\,m^{-2}\,h^{-1}$ were detected. In total six fluxes exceeded $100\,\mu g\,N_2O\,m^{-2}\,h^{-1}$, of which three occurred in HN plots, two in HNP plots and one in P plots. The average N_2O fluxes during the measurement period were 24.4, 10.9, -16.1 and $-6.1\,\mu g\,N_2O\,m^{-2}\,h^{-1}$ for
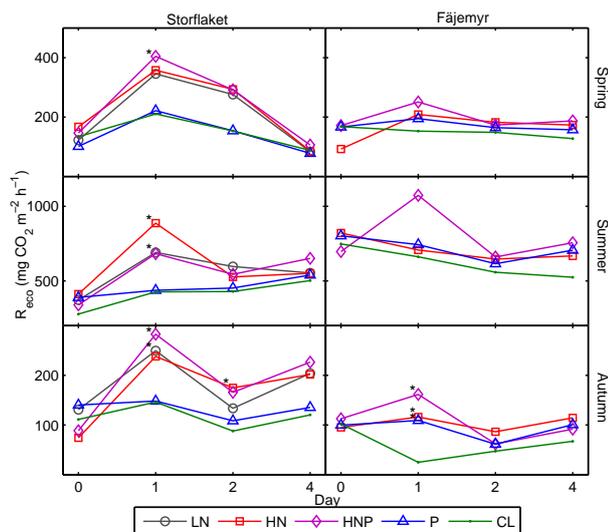
Fig. 2. Average R_{eco} (ecosystem respiration) rates ($n=4$) in all treatments in relation to the fertilization events in Storflaket (left column) and Fäjemyr (right column) in spring (top row), summer (middle row) and autumn (bottom row). Fertilization (on day 1 in graphs) was performed 24 May, 27 June and 23 September in Storflaket, and 30 March, 17 July and 23 October in Fäjemyr. Nutrients were added just before the GHG flux measurements were conducted on day 1. Asterisks show days when treatments are significantly different from control (two-sided Dunnett test: $p<0.05$). To increase visibility of the fertilization response with time y-axes scales differ between periods.

HN, HNP, P and C plots, respectively. There were no significant differences between these averages (ANOVA: $p=0.256$).

3.4 Repeated measures ANOVA

Statistics from the repeated measures analysis (RM-AN-OVA) and estimated marginal means (average fluxes adjusted for covariates, if any) are shown in Table 1. In Fäjemyr, there was a significant treatment effect on GPP ($p=0.026$). Phosphorus fertilized plots constantly showed higher GPP rates than plots that did not receive P (Table 1). In summer, all nutrient addition treatments had higher GPP rates on average compared to the control, while in spring and autumn the rates in HN plots were similar to CL plots. There was no significant treatment effect for R_{eco} ($p=0.272$), even though average values were always higher for fertilized plots than CL plots. A similar picture appeared for NEE ($p=0.150$), where P plots tended to have a continuously higher net CO_2 uptake. There was a close to significant treatment effect for the CH_4 exchange ($p=0.091$). Nitrogen and P alone slightly increased CH_4 emissions compared to CL, while their combination (HNP plots) caused a counter-intuitive decrease in CH_4 emissions.

In Storflaket, both GPP ($p=0.001$) and R_{eco} ($p=0.018$) had statistically significant treatment effects. Nitrogen plots

had the highest rates of both GPP and R_{eco}, while average flux rates in P plots were similar to CL plots (Table 1). There was a strong tendency that fertilization decreased NEE in Storflaket ($p=0.056$), because GPP increased more than R_{eco}. There were also significant interaction effects between time and treatment for GPP and NEE in Storflaket ($p<0.05$, data not shown), indicating that the different treatments responded in dissimilar ways to nutrient addition during the measurement period. The CH_4 emissions were relatively low in this site and spatial variation was high, which led to no significant treatment effect ($p=0.690$).

3.5 Regression modelling

The nonlinear regression models showed good performance in explaining the variation in R_{eco} and GPP in each plot in Fäjemyr; r^2 values range between 0.72–0.95 and 0.65–0.96 for R_{eco} and GPP, respectively (Table 2). Soil temperature was always a significant variable in explaining R_{eco}. Water table depth was significant in 13 out of 16 plots, constantly showing a negative correlation with R_{eco}, indicating that lowered water table leads to increased respiration.

The resulting sums of the time series modelling of GPP and R_{eco} in each plot in Fäjemyr between March and November 2007 correlated significantly with shrubs (p equalled 0.002 and 0.003 for GPP and R_{eco}, respectively). Since this effect is not related to the fertilization treatments, the sums from each of the 16 plots were detrended using the residuals from the regression analysis with shrubs as independent variable, and then the average flux was added. This procedure removes the trend associated with shrubs, but does not affect the average fluxes.

The sums of the time series modelling of R_{eco}, GPP and NEE averaged over all plots in Fäjemyr between March and November 2007 were 634, -509 and 125 g C m^{-2}, respectively (Fig. 3). These numbers take the seasonal and diurnal dynamics in CO_2 exchange into account, as opposed to the numbers in Table 1, which show instantaneous daytime rates. As was the case for the RM-ANOVA analysis, there was a significant treatment effect for GPP ($p=0.009$), and Dunnett test showed significantly different GPP sums for P and HNP plots compared to CL plots (p equals 0.003 and 0.035, respectively), while GPP sum in HN plots was not significantly different ($p=0.102$). For R_{eco}, no significant treatment effect was found ($p=0.251$), even though fertilized plots on average respired more CO_2 than CL plots. Nor was any significant treatment effect found for NEE ($p=0.292$).

4 Discussion

The vegetation inventories showed no major shifts in vegetation distribution during the two year fertilization period, with the exception of shrub increase in HNP plots in Storflaket. The increased nutrient availability may have caused

Table 1. Statistics from the repeated measures analysis (RM-ANOVA) including covariates (upper panel); and CO_2 component fluxes (NEE, R_{eco} and GPP, mg CO_2 m^{-2} h^{-1}) and CH_4 flux (mg CH_4 m^{-2} h^{-1}, lower panel) from Fäjemyr and Storflaket. F and p values refer to treatment effects. Flux values are estimated marginal means (adjusted for covariates, if any, listed in upper panel).

	Fäjemyr				Storflaket			
	NEE	R_{eco}	GPP	CH_4	NEE	R_{eco}	GPP	CH_4
RM-ANOVA								
F	2.17	1.51	4.56	2.78	2.93	4.28	8.43	0.57
p	0.150	0.272	0.026	0.091	0.056	0.018	0.001	0.690
Covariates	T_s	Shrubs T_s	Shrubs	Sedges	–	Vascular	Vascular	–
FLUXES								
Spring								
LN	–	–	–	–	−123	214	−327	0.32
HN	−141	210	−359	0.46	−133	233	−366	0.17
HNP	−205	255	−452	0.34	−122	242	−352	0.25
P	−204	222	−428	0.46	−187	141	−333	0.24
CL	−176	203	−377	0.42	−151	161	−330	0.21
Summer								
LN	–	–	–	–	−612	561	−1158	0.15
HN	−372	678	−1035	1.62	−679	631	−1310	0.32
HNP	−346	737	−1097	1.22	−768	601	−1347	0.32
P	−407	683	−1087	1.51	−531	527	−1066	0.22
CL	−275	604	−883	1.41	−536	512	−1078	0.30
Autumn								
LN	–	–	–	–	−109	170	−289	0.17
HN	−227	151	−375	1.25	−172	172	−344	0.50
HNP	−251	177	−435	0.63	−134	178	−326	0.38
P	−275	188	−456	1.08	−89	138	−222	0.28
CL	−204	146	−350	0.71	−96	134	−211	0.45

NEE, net ecosystem exchange; R_{eco}, ecosystem respiration; GPP, gross primary production; T_s, soil temperature at 5 cm depth. Positive values represent emission to the atmosphere, negative values represent uptake by the ecosystem.

changes in the competitive pattern in the ecosystems, but such changes are not yet detectable. Accordingly, this study reports effects on the greenhouse gas exchange dynamics that are not derived from vegetation shifts, but instead from biochemical and microbial responses to fertilization.

Gross primary production and R_{eco} in both sites correlated significantly with the amount of vascular plants (also amount of shrubs in Fäjemyr). Higher abundance of vascular plants, at the cost of mosses, leads to higher CO_2 flux components. However, these indices may also act as a proxy for biomass or LAI, which is known to correlate with GPP and R_{eco} (Lindroth et al., 2007). For CH_4, there was a significant correlation with sedges in Fäjemyr, and close to significant for Storflaket. Sedges (*E. vaginatum*) have an additional transport pathway through their aerenchymateous tissue (Joabsson et al., 1999) for CH_4 to escape from the anaerobic zone directly to the atmosphere, and hence avoid being oxidized to CO_2 in the aerobic zone of peat profile.

A short-term (hours to days) response in R_{eco} to nutrient addition was generally seen in both sites (Fig. 2). Although the addition of water during dry conditions may have stimulated microbial activity, the effect was prominent only in plots receiving nutrients. Due to the short-term nature of the response, we believe that nutrient-limited soil microorganisms were responsible for the increased CO_2 effluxes, which demonstrates the potential for higher decomposition rates in conditions of alleviated nutrient limitation. This interpretation is also supported by the lack of effect on GPP. Berg and McClaugherty (2003) discuss that early stage decomposition of easily decomposable material is stimulated by high levels of major nutrients (N, P, S), while in a later stage when degradation of lignin controls litter decomposition, N may even have a suppressing effect on degradation. Thus, when nutrients were added to the plots, there was an increase in decomposition of easily decomposable material. After some time, in combination with decreased nutrient availability due to plant uptake, the fresh C substrate pool became exhausted and the stimulating effect of increased nutrient availability ceased. Whether decomposition becomes suppressed in the long term (Berg and McClaugherty, 2003), can not be seen in our data.

Table 2. Estimated parameters from Eq. (1) and Eq. (2) used to model seasonal time series of GPP (gross primary production) and R_{eco} (ecosystem respiration) in Fäjemyr. NS: Not signficant (see Sect. 2.5).

| Plot nr | Treatment | GPP | | | | R_{eco} | | | | |
		b_0	b_1	n	r^2	b_0	b_1	b_2	n	r^2
1	HN	−87	273	18	0.95	3.75	0.126	−0.0061	15	0.95
2	HNP	−87	191	19	0.87	4.57	0.119	−0.0017	16	0.89
3	CL	−87	329	21	0.76	4.37	0.105	−0.0035	18	0.92
4	P	−75	65	20	0.82	3.11	0.111	−0.0074	16	0.92
5	HNP	−62	41	18	0.81	4.61	0.124	NS	15	0.84
6	CL	−78	196	20	0.93	3.04	0.129	−0.0067	16	0.94
7	P	−79	35	20	0.78	4.62	0.129	NS	14	0.90
8	HN	−59	85	20	0.88	3.20	0.120	−0.0064	17	0.92
9	HNP	−158	819	18	0.94	2.88	0.147	−0.0108	15	0.96
10	P	−183	1173	20	0.93	2.89	0.146	−0.0094	15	0.96
11	CL	−71	546	20	0.65	3.43	0.087	−0.0036	17	0.82
12	HN	−111	343	20	0.91	4.14	0.128	−0.0025	16	0.93
13	P	−71	114	16	0.72	4.74	0.096	NS	14	0.73
14	CL	−59	164	19	0.78	3.81	0.143	−0.0020	17	0.80
15	HNP	−100	657	19	0.78	2.77	0.130	−0.0074	17	0.90
16	HN	−118	281	20	0.88	3.65	0.130	−0.0054	17	0.90

Both in the RM-ANOVA analysis and the regression modelling, it was found that P was significantly stimulating photosynthetic CO_2 uptake in Fäjemyr. The increase was ca. 36% as compared to the CL plots as calculated from the GPP time series sum. Nitrogen addition also seemed to stimulate growth, but mainly during summer (Table 1). This may be because *Sphagnum* mosses represent the main part of the ecosystem CO_2 uptake during the early and late part of the growing season. During summer, when the vascular plants are active, the relative importance of *Sphagnum* mosses is decreased. Earlier studies have found that *Sphagnum* does no longer capitalise on increased N input at high N deposition levels and that additional N will leach through the *Sphagnum* layer and become available for vascular plant uptake (Lamers et al., 2000; Rydin and Jeglum, 2006). Our GPP data from Fäjemyr suggests that *Sphagnum* mosses are not N limited, due to the similarity between N and CL plots during spring and autumn, but rather P limited. It also suggests that the *Sphagnum* filter fails (Lamers et al., 2000) and that N leaches down to the vascular plant root zone causing increased growth of vascular plants during summer. It can not be excluded that this already occurs in Fäjemyr at the present N deposition of ca. 15 kg N ha^{-1} yr^{-1}. In a longer time perspective, this may act to decrease the net C sink in this ecosystem (Berendse et al., 2001; Malmer and Wallén, 2005).

In Storflaket, GPP was significantly stimulated by N addition, while P addition had low or no effect. In addition, R_{eco} also showed a significant treatment effect with higher rates in N plots. In this area where N deposition is low, both plants and microorganisms are limited by N, while the addition of P does not seem to have any major effect. Our results,

based on a whole-ecosystem approach using in situ GHG flux measurements, support the findings of Aerts et al. (1992), who performed a comparable fertilization experiment also in Swedish mires that focused on *Sphagnum* productivity. Their results indicated that growth was mainly N limited in an area with low N deposition, while it was primarily P limited in a high N deposition area. However, in a four-year fertilization experiment (Aerts et al., 2001) no effects on productivity were found. They argue that nutrient addition may initially ease the nutrient limitation to plant growth, while in the long term other environmental factors become increasingly important.

The modelled CO_2 components in Fäjemyr (Fig. 3) in this study can be compared to flux data from a nearby eddy covariance measurement site (Lund et al., 2007). Sum of NEE, GPP and R_{eco} during the same period as the chamber measurements, calculated according to Lindroth et al. (2007), are −55.7, −548 and 492 g C m^{-2}, respectively. There may be several reasons for higher R_{eco} and similar GPP sums found in the chamber measurements. Firstly, the fertilization area is drier than the footprint area of the eddy covariance tower; higher respiration rates can, therefore, be expected. Secondly, photosynthesis may be underestimated in the chamber measurements since climate controlled chambers were not used. When measuring NEE with transparent chambers, photosynthesis may be reduced due to (1) humidity increases forming droplets on plant leaves preventing CO_2 uptake through stomata; (2) temperature increase inside the chamber during measurements will increase respiration rates to a higher extent than photosynthetic rates; and (3) the CO_2 concentration reduction inside chambers during measurements will affect photosynthetic uptake (Hutchinson
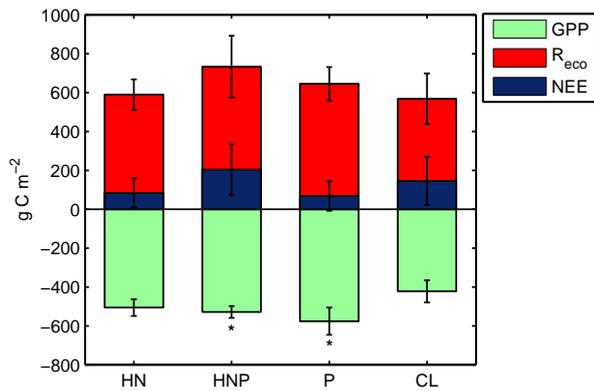
Fig. 3. Sum of modelled time series of GPP (gross primary production) and R_{eco} (ecosystem respiration), detrended for shrubs, and NEE (net ecosystem exchange), for the period March–November in Fäjemyr. Error bars depict standard deviation ($n=4$). Significant difference in GPP sums for HNP and P plots from control (Dunnett test: $p<0.05$) is indicated by a star.

and Livingstone, 2001; Welles et al., 2001; Kutzbach et al., 2007). Thirdly, there are also potential errors associated with eddy covariance measurements such as underestimation of respiratory fluxes due to vertical and horizontal advection (Baldocchi, 2003). Consequently, we believe that GPP is slightly underestimated in the chamber measurements while R_{eco} is accurate. This propagates into the estimation of NEE between March and November (Fig. 3) in which 14 out of 16 plots acted as a CO_2-C source to the atmosphere.

The measured rates of CH_4 emissions were fairly low in Storflaket and Fäjemyr compared with other Nordic peatlands (Saarnio et al., 2007). However, in Storflaket, measurements were conducted in a dry to semi-dry ombrotrophic habitat, which can be expected to have low CH_4 emissions due to the low water table and low productivity of the ombrotrophic community (Bäckstrand et al., 2008). Low CH_4 emissions in Fäjemyr may be explained by the fairly high amounts of nitrogen and sulfur deposition (Persson et al., 2004), which may cause a general limitation of methanogenesis (Whalen, 2005). No treatment effect was found for the CH_4 exchange, but the positive correlation with sedges indicates a potential for increased CH_4 emissions in the future, as sedges are thought to become more abundant if the nutrient limitation is reduced (Rydin and Jeglum, 2006). In Fäjemyr, P and HN plots showed on average (insignificantly) higher CH_4 emissions than the CL plots, while HNP plots did not show further increases in emissions as could be expected. However, the combined effect of single factor responses is often found to be non-additive (Shaw et al., 2002). For HN plots, increased CH_4 emissions may be associated with inhibition of CH_4 oxidation by methanotrophic bacteria. In HNP plots decreased emissions can be due to decreased plant root exudation rates, because of alleviated nutrient limitation, leading to decreased substrate availability for methanogenic archaea.

In addition to the gaseous C exchange, our data set indicates a possibility for increased N_2O emissions with increased N availability. Even though the flux measurements were performed at a low temporal resolution, several N_2O peaks were detected in N fertilized plots. These were likely associated with increased N availability for nitrifying and denitrifying bacteria, which signifies the importance of taking N_2O exchange into account when considering N fertilization as a means of increasing C sequestration in ecosystems, since N_2O is a strong greenhouse gas that may offset potential increases in CO_2 uptake.

5   Conclusions

– In accordance with our first hypothesis, GPP in the high N deposition site Fäjemyr was significantly stimulated by P addition, while in Storflaket, both GPP and R_{eco} were significantly increased in plots receiving additional N.

– No significant effects of nutrient addition were found for the CH_4 exchange, while N_2O peaks were detected in N fertilized plots.

– Future GHG flux exchange in nutrient-poor peatlands is dependent on changes in ecosystem structure such as plant composition due to increased nutrient availability, along with climatic changes associated with global warming.

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